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THE TRANSACTIONS OF THE ROYAL ENTOMOLOGICAL SOCIETY OF LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

CONTENTS

A collection of essays and scientific papers brought together to celebrate the ninety-fourth birthday of
KARL JORDAN

LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W. 7

Price £5 0s. 0d.

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THE
TRANSACTIONS
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ROYAL ENTOMOLOGICAL SOCIETY
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LONDON

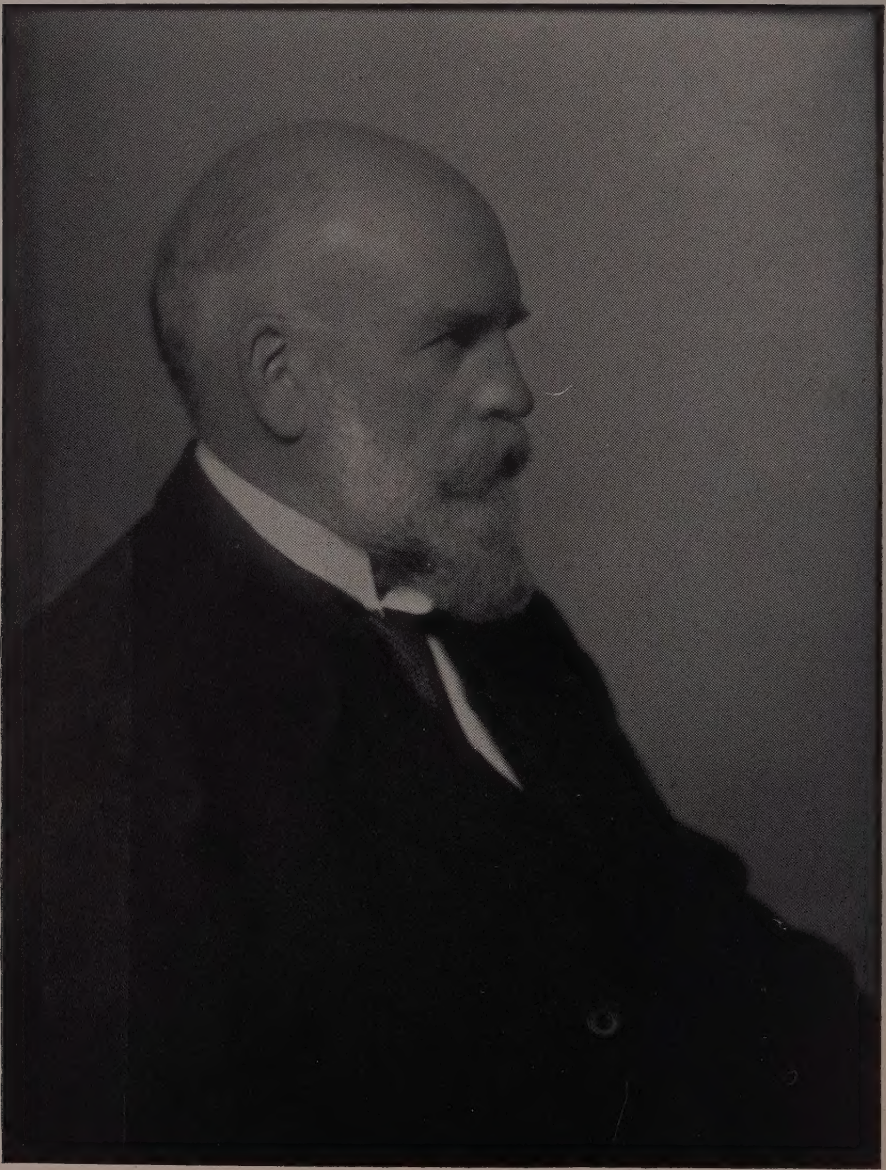
Vol. 107

A COLLECTION OF ESSAYS AND SCIENTIFIC
PAPERS BROUGHT TOGETHER TO
CELEBRATE THE NINETY-FOURTH BIRTHDAY OF

KARL JORDAN

LONDON
1955

Printed in England by Adlard & Son, Ltd.,
Bartholomew Press, Dorking.



Yours ever.

Karl Jordan K.J.

To

HEINRICH ERNST KARL JORDAN
PH.D., F.R.S.

HONORARY LIFE PRESIDENT OF THE INTERNATIONAL
COMMISSION ON ZOOLOGICAL NOMENCLATURE AND OF
THE INTERNATIONAL CONGRESSES OF ENTOMOLOGY

FORMERLY DIRECTOR OF THE ZOOLOGICAL MUSEUM, TRING

THIS VOLUME OF ESSAYS BY HIS FRIENDS AND ADMIRERS IS
GRATEFULLY DEDICATED BY THE ROYAL ENTOMOLOGICAL
SOCIETY OF LONDON IN RECOGNITION OF HIS OUTSTANDING
CONTRIBUTIONS TO ENTOMOLOGY

FOREWORD

I take great pleasure in presenting this volume in honour of Dr. Karl Jordan, F.R.S., on the occasion of his 94th birthday, in recognition of his unique contributions to entomology.

Dr. Jordan is an international figure and this is reflected in the origin of the volume. Mr. Harry K. Clench, of Pittsburgh, U.S.A., the initiator of the project, secured the interest of friends of Dr. Jordan in the U.S.A., Canada and Great Britain and, with them, laid the foundations for the volume and invited contributions. For practical purposes the Society was invited to undertake publication and assumed the responsibility with pleasure. I take this opportunity, on behalf of the Society, to express deep appreciation of Mr. Clench's initial work in launching the volume and for giving us the opportunity to carry on with it.

It will be unnecessary for me to enlarge here on the numerous facets of Dr. Jordan's activities. These are fully covered in the various Essays which, together with the Scientific Contributions here published, are a tribute to Dr. Jordan's 70 years of active work in and for our science. These contributions have been prepared by his friends and colleagues in the fields which have been his particular interest.

The list of publications given in the bibliography gives some measure of the extent of Dr. Jordan's studies and his outstanding contribution to entomology.

PRESIDENT.

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WITH FRONTISPIECE,
11 HALF-TONE PLATES, 6 LINE PLATES AND
272 TEXT-FIGURES

"My business is to teach my aspirations to conform themselves to fact, not to try and make facts harmonize with my aspirations."

T. H. Huxley *in litt.*, 1860.

KARL JORDAN—A BIOGRAPHY

Cat

Born 7th December, 1861.

K.J.'s father, a small yeoman farmer in Almstedt, a village south of Hildesheim, died when his youngest child was five. The story goes that his grandfather, worrying over the future of the seven children, was overheard muttering to himself: " One too many, one too many."

K.J. became the errand boy of the family. Out on the stubble fields at sunrise, he tended the geese or herded the cows in the meadows and along the grass verges. He learned a lot about the practical side of farming, and helped his eldest brother with the reaping and sowing, ploughing and harrowing. It was a simple, very care-free life. There was plenty of time too for following his own inclinations—bird's nesting, fishing in the brook with a basket, and catching three different kinds of little fish, and when there was a plague of field voles damaging the crops the boys, with home made wooden traps and great zest and considerable skill, caught as many as two hundred voles a day. If they had fleas, K.J. did not notice them.

His older brothers considered Karl a bright boy—he was a voracious reader and pored over books and atlases with tremendous concentration. It was felt that he should, if possible, go to the Hildesheim High School (Realgymnasium), but in order to pass the entrance examination he needed coaching in Latin and French. The problem was solved by his uncle, a prosperous farmer who lived in Sibbesse. He called one day in the autumn of 1873, and hearing of the difficulty he invited Karl to live with him, and promised to arrange the necessary coaching. The winter went by and spring came at last, but nothing further was heard of the plan. K.J. became anxious. One morning, after a word with his mother, he set off from Almstedt alone leaving his favourite ridge of bilberry-clad hills to the north, and with the rising sun behind him started on the long walk to his uncle's farm. On arrival he hung about, awkward and silent. " What is Karl doing? " said his uncle suddenly about mid-day: " He seems to have been around here all morning. Hey, boy, what are you up to? Have you come with a message from your mother? "

" No ", said K.J. with great embarrassment: " I have come—I have come—about the High School and the extra coaching you spoke of." The uncle was astounded—he had quite forgotten—but he and his wife responded generously; the coaching was arranged and Karl moved to his uncle's house. At fourteen, he was able to enter the Hildesheim High School. He then left the farm and for the rest of his school career shared rooms in a tobacconist's shop with a fellow student from a village nearby.

During his first holidays at home, his second brother, who was an elementary school teacher and something of a naturalist, took him collecting beetles in the woods nearby. K.J. from earliest childhood had been interested in both plants and animals, and had also collected various specimens for himself which were preserved in Schnapps in glass jars, and thrown away when they began to smell. On this particular afternoon among the captures were several specimens of the longicorn beetle, *Strangalia armata*. K.J. was thrilled; at that moment his whole future was decided.

All naturalists and keen collectors are familiar with the wishful dream which from time to time tantalizes the soundest sleeper; on his ninetieth birthday someone asked K.J. what he tried to catch on these occasions. "Beetles", he replied without a moment's hesitation: "Beautiful beetles with tough elytra, crawling near the base of the trees in the woods at Almstedt."

Perhaps one of his greatest qualities is single-mindedness. It runs like a steel thread through his life and his work.

In 1882 K.J. entered the University of Göttingen and in 1886 took his degree in Zoology and Botany—awarded the coveted Summa cum Laude in the gruelling oral examination for the Ph.D., and a year later acquiring a teaching diploma. He then interrupted his career for a year's military service. He was a good recruit and rather enjoyed soldiering. In those days the one year voluntary trainee had to pay for his uniform, including boots and helmet, and also provide his own food and lodgings. K.J.'s brother advanced the money, but it did not come very regularly and sometimes he went hungry. "It did no harm," wrote K.J. "Evidently I was tough."

When military service ended he went as a "probandus" to the grammar school at Münden, where he remained five years and in the autumn of 1892 accepted the post as master of mathematics, physics and natural history at the School of Agriculture at Hildesheim.

Eventually, in 1891, he was able to marry; he and his wife had fallen deeply in love while still in their teens, and they remained absolutely faithful to one another. It was a very happy marriage. He also found teaching boys much to his liking. He thoroughly understood his pupils. To put things lucidly and well for the benefit of the student or beginner has proved one of K.J.'s greatest gifts. He has never been too busy to reply either to the written or the spoken query. Those innumerable letters to students of entomology, so miraculously to the point and so generously detailed (typed, apparently, on yellowing tissue paper with a ribbon long overdue for the wastepaper basket), have become justly famous. They make very good reading.

It seemed at this time, however, that K.J.'s future was clearly mapped out and that he was destined for a sound, perhaps even eminent, career as Professor of Zoology in the Academy of Forestry. Then came the invitation to Tring.[1]

It is difficult to envisage a queerer state of affairs than that which K.J. found at Tring when he arrived there in 1893. Walter Rothschild was then twenty-four years of age and a most eccentric figure. He was always just about to leave the Rothschild banking house in disgrace, not for any serious misdeed, but because he displayed a quite remarkable lack of business acumen coupled with curious but very extravagant tastes, and—worst of all—while pretending to attend the House of Commons actually spent all his time at the Natural History Museum! From the age of seven years he had been an ardent collector, but he also possessed that genuine, rather naïve enthusiasm for animals which characterizes relatively few zoologists. He went up to Cambridge accompanied by a large flock of kiwis, and could be seen bowling down Piccadilly behind four lively zebras. He was endowed with a most remarkable, somewhat freakish memory which retained the specific characters of large groups of animals and enabled him to pick out, instantly, any new species without recourse to the relevant literature. His collecting was also a trifle eccentric; he was for instance obsessed by size and felt impelled to collect—at whatever cost—the largest sponge, the largest tortoise, the largest ape and the like for his museum. He himself was a large man with an enormous head, standing six feet three and eventually attaining a weight of three hundred pounds. In addition he suffered from a peculiar impediment in his speech together with a certain inability to control his voice, so that he alternately spoke with an embarrassing stammer or in a loud bellow. Although he was essentially gregarious and jolly, with boundless good nature, this physical disability, coupled with the knowledge of his father's constant, bitter disapproval of everything he did or liked, had made him shy and uncouth in society. In a sense he never grew up, remaining all his life the truant, rather irresponsible schoolboy, escaping with his butterfly net and pill boxes into the fields, and in later life secretly buying the largest boa constrictor in the world when his curators at the Museum were urging the purchase of some less spectacular but more important addition to the collection.[2] Yet Lord Rothschild was both so very peculiar and so very kindly, and also so richly endowed with those nameless qualities which combine to make a natural gentleman, that all those who knew him well liked him and found him delightful, and those with whom he came into daily contact grew, as time went on, increasingly fond of him. Everyone was always astonishingly ready to rally round and take responsibility for the latest scrape, whether it entailed coping with cassowaries or chorus girls, a final income tax demand or a hungry iguana. Moreover, working with him was always easy, even if at times it must have appeared to his curators like a partnership with a rogue elephant!

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[1] At the Hildesheim High School K.J. had been fortunate in having Wilken—a keen botanist and coleopterist—as his teacher in natural history. At Münden he was again lucky to strike up a firm friendship with two rather outstanding personalities, A. Metzger, the Professor of Zoology at the Academy of Forestry, and Count Berlepsch, a well-known ornithologist. Both these men had recognized his ability, welcomed him to their homes and had widened his outlook on life as well as on biology. It was at Count Berlepsch's house that he met Ernst Hartert, with whom he exchanged views and who eventually sent him the invitation to Tring. Dr. Hartert himself had only recently been appointed Director of the Tring Museum, recommended for this post by Albert Gunther. In a way Lord Rothschild possessed a sort of Midas touch where the selection of his Museum staff was concerned. In the light of to-day we can see that for a man interested in the systematics of birds and insects—and it must be recalled that he was only twenty-four years of age at the time—it was manifestly impossible for him to find two better men than Ernst Hartert and Karl Jordan.

Another equally disconcerting aspect of the situation at Tring was the complete lack of facilities for working with a microscope. Walter Rothschild's father had recently erected two cottages on the outskirts of the park in which his son was supposed to house his museum, but there was no space to accommodate the 300,000-odd beetles which K.J. was engaged to "arrange, determine and classify". This gigantic overflow was stacked in boxes at random and in fearful confusion, in sheds and hired rooms scattered about Tring. K.J. had not even a suitable desk at which to work, and found it necessary to retire to the landing window-sill if he required sufficient light by which to use so much as a powerful lens. But this weird state of affairs in no way disconcerted him ; with characteristic objectivity he appreciated the immense opportunities Tring had to offer. Here was the chance for both interesting and creative work. He took it.

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[2] W.R. was also a miraculous collector of books. In his article "In Memory of Lord Rothschild" Dr. Jordan dismisses this subject with a touch of asperity. "The Library of the Museum contains a number of rare old books on travel and natural history of little use for systematic zoology. . . . " I fear that at least one student of the flea has spent many an unprofitable but vastly agreeable afternoon in the Museum library marvelling over Moses Harris's original drawings for the Aurelian and similar unique volumes. Dr. Jordan's irritation was, however, understandable; there was never any surplus money available for running the Museum!

It is an almost incredible fact that within a year the collections of over 300,000 beetles (60,000 species) were arranged and classified—in the more conspicuous families named down to genera and species—while by the end of the following year over 400 new species had been described. K.J. was quick to realize that one aspect at least of Walter Rothschild's mania for size was both important and valuable. It was only a large collection such as this, containing both a great number of species and very long series of specimens, which could give him the facts he required.

The hours of work were theoretically from 9.0 to 4.0, but as the hopeless task of teaching Walter Rothschild high finance had not then been entirely abandoned, he himself rarely managed to arrive at Tring before six o'clock, and consequently K.J. often spent fourteen hours or more at the Museum. After dinner his wife usually accompanied him, and for half the night was content to sit by his side and help him with the labelling of specimens. Officially the annual holidays were six weeks, but K.J. only took one every other year, when he returned to visit his family in Germany. He had no hobbies outside zoology, and his only relaxation was a long walk or bicycle ride on a Sunday afternoon. After the age of fifty, however, he became a keen gardener.

In 1894 Walter Rothschild suddenly decided that he must have K.J.'s assistance with the Revision of the Papilionidae which he was then planning. Tongue-tied and with a guilty conscience about switching his curator from beetles to butterflies, he was quite unable to broach the subject directly. He decided that perhaps the simplest way was to hold up the supply of new beetles, and he therefore secretly instructed his collectors abroad to retain the Coleoptera for the time being.[3] K.J. soon realized what was afoot, but made no bones about abandoning the beetles and forthwith began work upon the Swallowtails. Up to that day he was familiar with only the two common European species. At any rate he was now given a desk with an excellent light.

One soon grows accustomed to advances, great and small, in any scientific field, and, in fact, rapidly takes them for granted. At a distance of sixty-odd years one fails, perhaps, to appreciate what a great step forward the revision represented. At the time it broke entirely fresh ground and supplied the data for a new approach to the problems of micro-evolution in the Lepidoptera.

Before K.J. had won himself a desk on the ground floor of the Museum Cottage he was sometimes joined at the landing window-sill by a modest but very enthusiastic schoolboy for whom he instantly conceived a great liking. Thus began the only real friendship of his life in England. He always got on well with boys, and in his company Charles Rothschild—Walter's younger brother—felt marvellously at ease. Questioned once about the discrepancy in their ages,[4] K.J. brushed this aside with a smile and replied simply : " He was so nice ".

[3] It must be confessed that during the past few years both G. H. E. Hopkins and the writer of these lines have often wished that the supply of beetles were not so limitless !

[4] At this time K.J. was exactly twice the age of C.R.

For the next thirty years the story of K.J.'s life was largely the story of his work at the Tring Museum and his relationship with these two brothers, both naturalists, both gifted, but with strangely dissimilar characters.

It is said elsewhere in this volume that K.J.'s ability was never fully appreciated by his contemporaries ; however true this may be, it does not apply to Charles Rothschild,[5] who not only admired him profoundly but never ceased, in speech and in writing, to point out K.J.'s genius and to stress his contribution to biology. " Jordan is the cleverest man I know " was a phrase with which the writer early became familar.

Both men were clear and objective thinkers possessed of great intellectual honesty, and their broadminded, tolerant views on politics, philosophy, religion and human affairs in general coincided. They were both reserved, modest, kind and unselfish, both devoted to their wives and families, both great lovers of nature, and gifted field naturalists. When together they found keen mutual happiness in collecting their specimens and discussing the scientific problems that arose in their own particular fields. K.J., however, was endowed with superb health of both body and mind—sadly lacking in his brilliant but over-sensitive, over-anxious, nervously-strung partner. When in 1916 following an attack of " Spanish influenza " and suspected encephalitis lethargica, Charles Rothschild became a desperately sick man, K.J. left the Museum and his wife and daughters to spend over two years with him (and later a further period of six months) in Switzerland, without once returning home, in a temporarily successful endeavour to nurse him back to health. Four years later, however, when he was staying with his friend at Ashton, Charles Rothschild suddenly turned the key in his bedroom door and killed himself. K.J. never wholly recovered from this bitter blow. To the onlooker it seemed as if he had suddenly grown strangely remote, apart, lost in thought, pondering some insoluble abstract problem. He often sat thus for long periods in silence, apparently quite unaware of his surroundings as if a sheet of glass separated him from the outside world, with his head flung back and his beard tilted at a slight angle. Although this phase was only temporary, to those who knew him really well K.J. never again quite lost a faint air of remoteness. In later years deafness greatly accentuated this impression.

A few days after C.R.'s death he returned to his desk and the routine of the Tring Museum, to the mass of new material that continued to flow in, to the piles of correspondence, to International Congresses and to Zoological Nomenclature, and for the next twenty-odd years to tend to Walter Rothschild with tact, good humour and affection.

In 1911 Karl Jordan decided to adopt British nationality. He always preserved a sound but agreeably sentimental attachment for the country of his birth—scene of a happy childhood and a happy love affair set against the background of a frugal but satisfying life on the farm. Intellectually, however, he preferred England, and especially the English style of life. The outbreak of the 1914–18 war was a blow to almost all scientists, but truly internationally-minded men like K.J. were rendered particularly unhappy. He regarded the war as terrible enough, but frankly expressed the opinion to Charles Rothschild that a victorious Germany would prove still more disastrous for mankind. At that time anti-German feeling ran high in this country. It was quite a different atmosphere from that of World War II, when a clash of ideologies masked the clash of nationalities. In 1914, even in a small backwater like Tring, insults were shouted at foreigners in the streets and daily life was made difficult and at times painfully unpleasant. He understood all this, but he suffered because it depressed his wife—already cut off from her home and relatives. In various other ways, of course, the war hampered those activities in which he was particularly interested. K.J. had instigated and organized the first International Congress of Entomology held in Brussels in 1910, but the third meeting was cancelled and he only succeeded in reorganizing it thirteen years later at Zurich in 1925. He remained its permanent secretary until 1948, and became thereafter an honorary life president. K.J.'s great modesty and sincerity, his supremely tolerant and impersonal but very kindly outlook, marked him out as ideally suited for renewing international contacts and, very quietly, he rendered a great service in this field. At congresses he became a familiar and universally-popular figure[6]—acquiring the sort of popularity we should all so much like to enjoy, but rarely achieve outside the realm of daydreams.

---

[5] Nor for that matter to Walter Rothschild.

" How do you get on with Jordan ? " asked Dr. Nissen shortly after his appointment at Tring. " We have terrific arguments," replied Lord Rothschild with engaging candour : " but the fellow is always right ! "

The author once pressed Lord Rothschild's mother, then a formidable old lady of over ninety years, for her impression of Dr. Jordan when he first arrived. " Ah, old Jordan," sighed Lady Rothschild, who despite the fact that he was twenty years her junior persisted in referring to him thus : " Old Jordan . . . he was so extraordinarily good looking, I can't recall anything else ! "

In 1913 he was appointed a member of the Commission for Zoological Nomenclature,[7] another sphere in which the war greatly interfered with progress. In the same year E. B. Poulton proposed him for the Royal Society, but on the outbreak of war he was well advised to withdraw his name from the list of candidates. It is a rather curious fact that he was not proposed again—this time by Sir Guy Marshall—until 1932, when the election, so long overdue, eventually took place. The war, as we have seen, also forced upon him a most difficult decision. In 1916 he chose to accompany Charles Rothschild to Switzerland, which meant leaving his work and his family for what then seemed an indefinite period. Unhappily, on his return home two years later he found his wife a sick woman. She never entirely recovered her health, and died in 1925. Finally the war took a heavy toll of private fortunes, particularly those with interests abroad, and this factor, coupled with Walter Rothschild's freakish extravagances, meant that from the end of hostilities onwards the Tring Museum was faced with a greatly reduced budget, and the necessity for keeping expenses within strict limits. How Jordan managed to organize the department of entomology (and from 1930 onwards the whole museum)—all the time adding to the collections and maintaining the level of scientific output—with the greatly reduced funds at his disposal was something of a miracle. His desk, with the microscope, typewriter and camera lucida, almost buried beneath a welter of books, papers, tins, tubes and glass-topped boxes full of specimens—the latter apparently defying the laws of gravity for weeks on end—presents a most deceptive impression of disorder and confusion.[8] In all essential matters, whether they concern the administration of the museum, the organization of a collecting trip or some minor question of nomenclature, K.J. is clear, decisive and orderly. Perhaps the most unfortunate aspect of the museum's financial troubles was the fact that K.J. felt it necessary to carry out a mass of menial tasks himself. The writer of these lines was appalled to find (in 1938) that he personally labelled every figure in the Museum publication, *Novitates Zoologicae*! K.J. was a rapid worker and he reckoned that it took him on an average sixteen hours to describe a new flea or beetle, and one greatly regretted the time he spent in tying up parcels of specimens lent to other institutions, and similar chores. Always unselfish, he put what he considered were the interests of the collection first. In his article in memory of Walter Rothschild he generously credits him with the entire creation of the entomological department at Tring. It would be truer to say that Walter Rothschild, who amassed the collection with great zest and enthusiasm, was quick to appreciate and act upon the many shrewd suggestions made by his curator. Thus it was K.J. who in the very early days insisted upon accurate and detailed labelling of specimens, the dissection—especially of the genitalia—of newly-described forms and the emphasis upon that side of the collection which went beyond the mere registration of species. "Systematics are the basis necessary for the solution of biological problems[9] and must be sound." Walter Rothschild was guided by these principles, and thus the collection of over two-and-a-half million butterflies and moths became one of the most valuable in existence.

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[6] To his English friends his strong German accent, which has never been the slightest degree softened by time, is one of his many endearing features.

[7] He was president of the Commission from 1928 to 1948, and remains an honorary life president.

A glance at the bibliography (p. 77) shows that up to date K.J. has written over 460 papers. Most of these publications concern the systematics and distribution of beetles, butterflies and moths and fleas, but many of them—for example "Where subspecies meet"—reveal the author as not only a first-class systematist but also a fine collector and field naturalist. After the war K.J. found time for an annual collecting holiday with his daughters—about six weeks—generally in the mountainous areas of Europe that he loves—the Pyrenees, the Alps, the Dolomites and so forth, but there were also visits to Algeria, the eastern U.S.A. and many districts in France, and at the age of seventy-four a major and very successful expedition of seven months' duration to South-West Africa and Angola. K.J., however, is just a little too good at his desk, and was rarely if ever spared to take part in the various collecting expeditions organized from Tring—a short-sighted policy that many of us greatly regret. K.J.'s phenomenal knowledge of physical geography and climate is a great help to him both in planning his collecting and interpreting the results, but like Charles Rothschild he also possesses that curious ability for instinctively recognizing a "good" collecting spot. One amusing example of this special gift occurred quite recently. It was a pouring wet afternoon in June, and K.J. had elected to go for a walk in the woods at Ashton. The walk began with a short lecture on the various parasites of hornets—the hornet having recently extended its range to Ashton—but conditions were depressing and, after a while, K.J. fell silent and continued to trudge onwards, head bent against the downpour, the rain dripping from the brim of his hat and his eyes fixed upon the ground, apparently lost in thought. After about three-quarters of an hour he suddenly stopped, raised his head hastily as if startled by a loud noise, and remarked to his astounded companion: "This is a very good spot for butterflies." He had halted in a slight bulge in a woodland glade less than fifteen yards square—the only spot where, for some totally inexplicable reason, all the rarities for which Ashton Wold is noted have been found together. E. B. Ford once wrote: "The accomplished naturalist . . . reaches his conclusions by a synthesis, subconscious as well as conscious, of the varied characteristics of the spot weighed up with great experience. But this is a work of art rather than science." On this occasion it must be confessed the art savoured of nothing short of black magic!

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[8] I am certain, however, that K.J. rather enjoys a good muddle on a small scale, and finds the sight of his desk stimulating. He also takes a certain amount of pleasure in executing a perfect figure with the aid of a most abominably hairy pen, a half-dried-up bottle of ink and a broken and obviously useless architect's curve.

[9] At the moment he is engaged upon a revision of the difficult genus *Stenoponia*. There must have been very few men—either now or in the past—who at the age of ninety-three were able to work regularly at the microscope and execute their own drawings, as K.J. still does.

There is yet another art, associated particularly with systematic zoology, which K.J. has developed to a high degree—the art of mastering the literature. Unlike Walter Rothschild, who found relaxation in the most trivial forms of fiction, and Charles Rothschild who was constantly tempted away by some new line of thought, K.J. read only biology.[10] Nevertheless his reading was prodigious and rapid. When in 1894 he was switched suddenly from beetles to butterflies he "read everything written about the Papilios—in all languages—available in libraries in this country" and studied the morphology in detail, and the first part of the Revision (three hundred-odd pages) *appeared in print in* 1895! But we all know that a good memory and prodigious reading, however rapid and however wide, are not enough. The art that makes a master—the process of choosing, absorbing, assessing, remembering and forgetting and intuitively reading between and beyond the lines in the literature—defies analysis.

In the biological world, perhaps more than in any other, a man stands or falls by what he has published. It is the sphere of the printed word. In this particular field K.J.—a good fifty years ahead of his time—has won an unchallenged place, but it may be that his personal contact with his fellow men has made an even deeper and more abiding impression. This belongs to the realm of things that we know and feel, but which certainly lend themselves still less than the art of the field naturalist to painstaking analysis. Besides, we are all captivated by tremendous, boyish enthusiasm—an enthusiasm that makes K.J. at ninety-three seem considerably younger than most of us. It is a delight to find a man for whom life is still intensely interesting, and who so palpably enjoys it. We are grateful, too, for the inner tranquillity—a little of which, in his presence, we seem to borrow. We are charmed, also, by a fine physique and a fine mind. But born and living as we are in the century of comic strips and concentration camps, anxiety neuroses and atomic warfare, it is perhaps the good life that moves us most profoundly. Somehow our faltering faith in humanity is restored.

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[10] K.J. tells me this is not quite accurate. In his early days he read many novels in English, French and German, and now often reads and falls asleep over a detective story ". . . telling the person who regrets that Lady Isobel is so fickle that it is not Lady Isobel's fault, but that of the author. And then I am bound to ask whether our forebears are really responsible for what we do and think, and wonder whether the Lord Chief Justice would condemn anybody for having done something if the anybody had not the slightest idea that he had done the something . . . and if I am then still half awake I feel profoundly grateful to the host of my ancestors for the inheritance of this mixture of good, bad and middling that is me . . ."

M. R.

From Professor V. B. Wigglesworth, C.B.E., F.R.S.

University of Cambridge,
Department of Zoology,
Downing Street,
Cambridge.
22nd September, 1954.

Dear Dr. Jordan,

It is with the greatest pleasure that I take this opportunity of writing a few lines on the occasion of your " Jubilee Volume ".

When the late A. D. Imms started work at Cambridge, David Sharp said to him : " If you want your name to endure, you must do taxonomic work and not morphology—if you want to do this higher line of work [by which he meant morphology] I fear I can be of little help ".

To-day the " higher line of work " in Entomology is no longer Morphology, but Ecology and Physiology, and before long it will be all Biochemistry and Biophysics. But, of course, David Sharp was right. The foundation which will endure when all the summer palaces will have crumbled away is good Taxonomy.

To have laid such foundations is just one of your many claims to honour, which it is a privilege to be able to acknowledge on this happy occasion.

Yours very sincerely,

V. B. Wigglesworth

From Dr. R. E. Snodgrass.

U.S. National Museum,
Washington 25, D.C.
10*th February*, 1955.

Dear Dr. Jordan,

I am pleased to be able to join with others in sending you congratulations on your having passed your 93rd birthday. You are one of a few entomologists that make the rest of us feel young at 80. Personally you once gratified and encouraged me very much by your favorable comment in a letter on my " Skeletal Anatomy of Fleas ". One of my associates here had assured me that no flea specialist would *ever* accept my interpretation of the flea mouth parts.

Many years have gone by since I once met you here at the Museum in Washington, and I hope you may be granted health for further years of service such as you have already given to entomology.

With best regards, I am,

Very sincerely yours,

R. E. Snodgrass.

From Dr. Julian Huxley, F.R.S.

31, Pond Street,
Hampstead, N.W.3.
21*st September*, 1954.

Dear Dr. Jordan,

I am very glad to have this opportunity of contributing my mite to this volume in your honour. I am not competent to say anything about your immense work in the field of entomology but I would like to testify to the notable contribution you made to the clarification of the species concept and of micro-evolution in general, by your pioneer studies on geographical differentition. They paved the way for the rapprochement between taxonomy and genetics, which has been such a fruitful feature of recent biological work.

Yours sincerely,

Julian Huxley.

From Professor R. Goldschmidt.

University of California,
Department of Zoology,
Berkeley 4, California.
5th August, 1954.

Dear Dr. Jordan,

It is a pleasure and an honor to be permitted to contribute a few lines to your volume in token of an almost life-long admiration. It is true that I am not an entomologist, though I worked for 45 years with entomology and have bred and studied larger numbers of insects than many an entomologist by profession. But, taking the risk of disgracing an entomological volume I am ready to state that I do not see in you an entomologist either but a great zoologist and naturalist.

Compared with your venerable age, I am a rather youngish man ; but being, according to usual standards, much advanced in age I might claim the privilege of doing a little reminiscing. It is not probable that you remember when we met first, as you were already a well established scholar, while I was a young graduate student who looked up admiringly to the great scientists who assembled in 1901 at the International Congress of Zoology in Berlin and listened to their important papers. But this first meeting means so much now to me, because it initiated me into a field which later was to become highly important for my own work. I mean the taxonomy on the subspecific level and its importance for evolution, a field in which you are one of the great pioneers and classics.

It is true, that at that time, I did not yet realize the importance of your work, though as an ardent coleopterologist, I should have been interested especially in the entomological approach. The reason was that I, like other German zoologists, was specially impressed by the claims of a rather noisy mammalogist (Matschie), who shocked his contemporaries, taxonomists and non-taxonomists alike, by the claim that he could distinguish and name different kinds of lions and giraffes, one each for every small region of the area of their distribution. Everybody knew that a lion is a lion and a giraffe a giraffe and thus Matschie with his native Berlin wit and shocking manners became a laughing stock, though he was essentially right. If we—I mean the general zoologist, who at that time still knew taxonomy—had studied your work, we should have become convinced of what to-day is the recognized taxonomic basis of microevolution.

Actually I had the good chance to become acquainted soon afterwards with your basic work in Lepidoptera, a knowledge which ten years later (1909–1912) encouraged me to start the genetic analysis of the subspecific categories in order to explore their evolutionary significance. Thus you influenced an important phase of my work without knowing it.

As I am now at reminiscing, I may also mention what led me in the first decade of the century to your classic work. This was actually a generation before the time when the importance of your and others' pioneer work was recognized by most other geneticists and zoologists and was baptized " the new Systematics ". This name implied that for a long time non-taxonomists had looked down upon taxonomic work as a kind of stamp collecting, unaware of the great revolution of taxonomy that had been going on since the end of the 19th century, a movement in which you played such a conspicuous role. Between 1904 and 1910 F. Doflein had organized in Munich a weekly meeting biological club, which consisted half of taxonomists, including palaeontologists, and half of general biologists, zoologists, botanists and physiologists. Here the taxonomists discussed and demonstrated their material under the point of view which you had helped to establish as one of the pioneers. Thus the systematics of Kleinschmidt, Jordan, Matschie, Hofer and their followers destined to become the " new " systematics 30 years later had become with me *the* systematics before 1910, thanks to my fortunate surroundings. Without this knowledge and conviction I hardly should have dared to embark on a trip to Japan to look for the expected taxonomic entities for my genetic work. Thus, dear Dr. Jordan, you became one of my godfathers without knowing it. Possibly I told you later, when I had the pleasure of being your house guest in Tring? I hope I did ; if not it is fortunately not too late, and while digging up these reminiscences, I beg you to accept the expression of my gratitude and also of my admiration for all you have done for our beloved science of zoology, in a life work of which I mentioned, for personal reasons, only one single phase, picked from the huge and many-faceted contributions which you made in a singularly blessed life.

Yours sincerely and devotedly,

R. Goldschmidt.

KARL JORDAN AND THE INTERNATIONAL CONGRESSES OF ENTOMOLOGY.

By N. D. Riley.

In Dr. Jordan's own words " the idea of the usefulness of an association of some kind aiming at international collaboration among entomologists occurred to me in 1904 when I was in the Upper Engadine with the Hon. Walter Rothschild collecting mainly Lepidoptera ". The seed, however, was certainly sown earlier. Around the turn of the century Dr. Jordan had found it necessary to visit the Natural History Museums in Dublin, Paris, Brussels, Amsterdam, Berlin and Stettin and many of the large private collections on the continent, such as those formed by Charles and René Oberthur, Staudinger, Walther Horn, Piepers, Snellen and others. These visits were made for the purpose of studying the type specimens of Hawk Moths, *Charaxes* and Swallowtail butterflies in connection with the taxonomic revision of these groups upon which he was working jointly with the Hon. Walter Rothschild. He had clearly been impressed by the degree of isolation of the scientific men he met during his travels and in particular by the fact that hardly any of them were known personally to each other; the lingua franca and the universality of science that had characterised the middle ages had vanished and, although the extreme nationalism of Napoleonic times was gone, scientists tended still to be competitive rather than co-operative and lacked in large measure the personal contacts that bring such rich rewards. The Zoological Congresses held at Cambridge in 1895 and at Berlin in 1901, both of which Dr. Jordan attended, gave him the impression that, even if the entomologists could get together amongst themselves, there was an increasing cleavage between them and other zoologists. This was particularly marked at Berlin where, from all accounts, tempers ran high and even personal animosities were allowed to invade the realm of science, especially in matters concerning nomenclature.

As is so often the way, documentary evidence of the steps taken by Dr. Jordan to secure the help and co-operation of entomologists in his plan is not extensive. The original plan was evidently to form first an international association of entomologists which it was hoped would help to bring entomologists of all parts of the world into closer touch with one another. Secondly, this association when firmly established was to organise from time to time International Congresses following the pattern set by the zoologists. It was customary at Tring at this time to keep copies of handwritten letters by a process still in use sometimes in solicitors' offices; a typewriter was not available, and in any case Jordan regarded his pre-Congress activities as aside from his official duties and no copies of his earlier letters exist. It is only from the replies that a picture of his activities can be obtained.

The earliest letter in the file is dated 9th March, 1905, and is from Schulthess-Rechberg of Zürich who writes: " Neulich war unser Freund Standfuss bei mir . . . Ich theile vollständig seine Ansicht, dass nähere Fühlung unter den Entomologen aller Länder gewiss wünschbar ist und dass wir aber leider bis jetzt bei den allgemeinen Zoologen noch nicht das gewünschte Entgegenkommen finden. So weit also meine schwachen Kräfte reichen, bin ich gerne bereit zur Anbahnung näheren Zusammenschlusses der Entomologen meine Dienst zu leisten. Was nun die von Ihren geplante Zusammenkunft in der Schweiz anbetrifft . . ." But twenty years were to go by before Dr. Schulthess, as president, was able to make good his offer to welcome the Congress to Switzerland.

In 1906 further inquiries were started. The reception accorded the five-point plan that now emerges was decidedly mixed. De Meijere " obgleich kein besonderer Freund von Congressen " expressed a general agreement with it. Adlerz thought its only effect would be to bring together " Häufe von Krethi und Plethi ". Handlirsch in a long and witty letter (14th December, 1906) concluded that it was not the public or zoologists that needed reforming, but entomologists themselves ; and that a Congress might be very useful in exposing swindlers! Heller was much more helpful, " Bezüglich des internat. Entomologen-Congresses bin ich . . . gespannt . . . glaube dass das Unternehmen kein undankbares ist und schliesslich die getrennt-marschierenden Lepidoptero- Diptero- Coleoptero- und andere-Logen zu gemeinsamer Schlacht vereinigen wird . . ." Severin, who later was to be President of the very first congress, expressed enthusiastic support. Schouteden, Aurivillius, Everts, Ris and Horvath (who had tried to start a similar movement in 1899) were strongly in favour. From Gestro, Silvestri and Bezzi in Italy there came enthusiastic support, likewise from Bolivar, Sjöstedt, Forel, Klapalek. Ohaus doubts whether the founding of an international " Entomologen-Vereinigung mit gelegentlichen Congressen (the only clear reference to the association idea) uns weiterhelfen wird." René Oberthur who " applaudes des deux mains l'idèe, qui n'est pas neuve mais qui avait besoin d'être mise en pratique et soutenue par un homme compétent et susceptible d'attirer l'attention et la sympathie de tous les entomologistes " has clearly recognised the man for the job and like his better known brother Charles (" vous êtes l'entomologiste douè du sens le plus droit et du tact le plus sûr") gave it his warm approval. The warmest support of all, however, came from Walther Horn, a life-long friend and ardent admirer of Dr. Jordan and all his works.

During the early months of 1907 still further replies came in, all almost without exception strongly supporting the proposals. Van Rossum (9th January, 1907) suggests that the organisation should be built upon the existing Internationale Entomologe-Verein in Zürich, leading eventually to a Standing Committee which would organise the Congresses. Father Wasmann (4th January, 1907) accepting the plan whole-heartedly, proceeds to outline a scheme of Sections, pleading that more attention should be paid to subjects of wide interest, such as morphological adaptations and their biological reasons, evolution, phylogeny, geographical distribution, but illustrating his point exclusively by reference to the Paussidae. J. T. Oudemans (20th February, 1907) pithily remarks "Congresse sind, und viele Leute werden dem beistimmen, ausgezeichnet um Bekanntschaft zu machen mit andern Fachleuten. Um die Wissenschaft zu fördern giebt es viel bessere Mittel ". Kolbe, in welcoming the idea makes a strong case for the publication of a truly scientific journal of the very highest quality by the Association expected to be formed. Like many of his German and Austrian colleagues he strongly decries the activities of amateur collectors, especially in publishing records of captures as " science ".

This is curious. It does not appear in the correspondence from other sources. It can readily be believed that amateurs were more numerous in Mitteleuropa ; but were they any " worse " than their counterparts in France, Britain and elsewhere? The amateur often makes a discovery which it will repay the scientist to investigate. Was Mendel a trained scientist, and not the purest amateur?

In a letter from Bengtsson written from Lund on 2nd January, 1907, there occurs at last an actual quotation from one of Dr. Jordan's own letters. " Mit Ihrem Plan bin ich ganz einverstanden, und es freut mich sehr, dass ein solcher Vorschlag von Seiten hervorragender Fachgenossen in den grossen Culturländern entstanden ist. Es ist leider so gewiss, was Sie sagen, dass unsere schöne liebe Wissenschaft ' ein Stiefkind der Zoologie geworden ist ' und dass die Stellung der Entomologie nicht der Wichtigkeit der wissenschaftlichen und praktischen Ergebnisse derselben entspricht ". There follow approving letters from leading British entomologists, among them Poulton, Charles Waterhouse, F. D. Godman, Verrall, Dixey, T. A. Chapman, Tutt and Merrifield and, a little later, the replies from America, where the science, because of its largely economic orientation, was already developing on lines rather different from those traditional in Europe. The American and Canadian writers express themselves with a remarkably uniform choice of words as " heartily in favour " of the Congress idea ; most of them lament their remoteness from Europe. T. D. A. Cockerell succinctly states one of the handicaps of isolation when he remarks that to " one who lives far away from the great centres of entomology an organisation formed in the centres presents some undesirable features : it is necessarily dominated by those on the spot and we of the periphery get no representation and have no influence ". He especially would like to see an international organisation " which could publish in *one* series all the descriptions of new species . . ." So would many of us!

Many heartening letters reached Dr. Jordan from other sources in early 1907, including an invitation from Standfuss to hold the Congress in Zürich and a stream of letters offering and giving help and advice from the ever ebullient Walther Horn. Such indeed was the support received by Dr. Jordan and the confidence he inspired amongst his wide circle of entomological friends, that, on 1st June, 1907, he addressed to a number of national entomological societies a letter (*see* 1908, *Proc. ent. Soc. Lond.* **1907–08**, xxxviii–xxxix ; 1907, *Ann. Soc. ent. Belg.* **51** : 161–2), announcing that invitations to the first Congress would be issued that summer.

This circular received at once a warm welcome from Bouvier, Horn, Schouteden, Stichel, Standfuss, Rowland-Brown and Heinrich, secretaries of societies to which it had been addressed. It is clear, too, from these letters that Brussels was the chosen place and Schoutedèn, as active in good works then as now, stated expressly " we are quite ready to undertake the organisation ". From then on, however, for nearly a year the files of the Executive Committee are silent. No invitations were issued, no further announcement made, apparently only two letters were received during the whole of 1908, one, significantly, from Severin and making an oblique reference to this Congress in the phrase " Ici rien de nouveau, j'attends toujours un mot de M. Blanchard quant à la date! " The other from the faithful and indefatigable Walther Horn.

However, the plan was not dead. Dr. Jordan (*in litt.*) supplies the answer:

" Severin informed me that the Committee organising the World Fair at Brussels for 1910 . . . would greatly welcome scientific meetings of all kinds, extending to them financial help and facilities of various kinds. That settled the matter ". When this decisive piece of news reached Dr. Jordan is not to be discovered from the papers of the Executive Committee, but it would seem to have been some time in 1908, for in no other way can the sudden halting of all activities be explained.

The following year opens with a spate of letters from Severin to Dr. Jordan, showing clearly that Brussels had been chosen and 1910 was the date. " Besten Dank für Papiere und Brief. . . . Wir müssen sehen wieviel Geld wir als Unterstützung verlangen, damit unsere Anfragen eine direkte Solution bekommen . . . überall ist die Geldfrage wichtig." Then follow answers to questions Dr. Jordan had posed. A week later: " Lameere wurde zum 2-jährigen President der Entomologischen Gesellschaft gemacht, damit er in 1910 functioniren kann . . . niemand regt sich und ich bien sicher, dass 8 Tage vor dem Anfang wird es nöthig sein die Herren zu erinnern dass überhaupt ein Congress besteht . . . Um dies nun zu verhindern bin ich der Meinung ein definitives Comitè in 1910 zu ernennen, welches alles vorbereitet . . . Bevor dieses Comitè ernannt ist, können wir, Sie, Horn, Lesne, ein Holländer und ich, das jetzige Comitè bilden und die ganze Organisation in den Händen halten."

Dr. Jordan was indeed fortunate in finding in Brussels a man like Severin, active, business-like, shrewd and thoroughly practical, to get things really moving. " Sie müssen an einige reiche Gönner sich richten um ein paar hundert Mark für die ersten Circulare zu besitzen ".

Things really began to move, and in March, 1909, as recorded in the published *Proceedings* of the 1st Congress (p. 5, not in 1908 as stated on p. 7), a meeting under the chairmanship of Dr. Dixey was held in the rooms of the Linnean Society in London. The minutes of this meeting, in Dr. Jordan's handwriting, are extant. They are printed, with a good many small improvements and the addition of the circular that was later sent out, on pp. 7–20 of the same *Proceedings*, in the guise of resolutions adopted on the submissions of Dr. Jordan, whose initiative is recognised on p. 5. The most effective single action that this Committee took, however, was to appoint the ringleaders—Horn, Janet, Severin and Jordan—as an Executive Committee. Very large numbers of the circular (at £4 per 10,000 copies!) were printed and distributed ; what had been originally the Permanent Committee became what in fact it always had been, the Provisional Committee, and an array of Local Committees scattered throughout the world was set up and provided with detailed instructions as to their duties. These committees proved in the main to be stillborn, for obvious reasons. Froggatt for example, wrote from Australia " we have very few entomologists in Australia . . . I do not think we should enrol a dozen members ". However, the appointed chairmen of these committees did good work in many lands and subscriptions came to hand. By November Severin could report " Ich bin überhaupt jetzt ruhig über den Erfolg". Meanwhile Jordan and Horn had been mainly busy with the organisation of the sections, meeting a few personal difficulties in the selection of chairmen, but none that their tact failed to overcome. A future historian will be thankful to note that at about this time both Dr. Jordan (of whose letters there begin to be copies) and Walther Horn took to using typewriters. The first Congress was duly held, and was voted an unqualified success by all who attended. Its final acts included the establishment of a Permanent Committee with 130 members and an Executive Committee of six, namely Malcolm Burr, Dr. Jordan, Walther Horn, Lesne, Severin and H. Skinner. The former was clearly too big to be functional, and appears to have died a natural death. A resolution that seems to have suffered the same fate, for it has never once been observed, was to the effect that at the end of each Congress the Executive Committee should prepare a balance sheet which should be published in the *Proceedings* of the next Congress. The nearest approach to a balance-sheet that is to be found in the files is contained in a letter to Dr. Jordan (13th May, 1912) from Severin, who says that the receipts were approximately 16,427·5 Belgian francs, the outgoings to date 8,550, but that after paying for the printing of the *Proceedings* he will probably be in deficit.

Before the affairs of the First Congress had been settled up, work had to be begun on the second, due to be held in Oxford in 1912. The machine really never stopped turning, and it would appear from the files that Dr. Jordan was relieved of the main burden of organisation by Malcolm Burr, of whose prodigious activity there is, however, little trace in the files. Who was at the wheel, however, remains clear all the time. All went well till the eleventh hour, when Burr had to withdraw. Smoothly and naturally Dr. Jordan stepped in, took over, and, ably assisted by the secretaries of the local organising committee, just succeeded in getting out the Preliminary Programme in time for the reception on August 4th. As is evident from the Report of the Executive Committee (1914, *Int. Congr. Ent.* II (Oxford, 1912) : 117–125) he took a particularly important share in the Congress discussions which led to the setting up of an International Committee on Nomenclature, a worthy project that failed, however, to yield the results it merited. A curious fact that emerges from a perusal of the scanty papers relating to this Second Congress is that a serious attempt had been initiated, apparently by Malcolm Burr, to establish a standard list of abbreviations of author's names. There are long lists submitted by many well known specialists, yet nothing was brought before the Congress. It was perhaps as well, for there is much to be said for the modern practice of printing all authors' names in full, with the possible exception of Linnaeus ; unfamiliar abbreviations can be a terrible snare, as the writer of this article knows to his cost.

In a final characteristic short speech concluding the Congress Dr. Jordan pointed out that, even if entomologists held differing and sometimes seemingly antagonistic theories, they all sought the hidden truths which the study of differences between species both illuminated and obscured, and that the making of friendships, as at Brussels and Oxford, could, and often did, provide agreeable opportunities for reconciling them.

Then came the 1914–18 war. The Congress scheduled to be held in Vienna in 1915 under the presidency of Dr. Handlirsch had to be abandoned, and conditions in Vienna after the war proved unsuitable. Nearly ten years elapsed before Dr. Jordan judged that the wounds and bitterness of the war were sufficiently assuaged and healed to make it possible to hold another international gathering.

He had spent the whole of 1917 and 1918 in Switzerland as a companion to the Hon. Charles Rothschild, who was suffering from a severe nervous breakdown. During this period he contacted many Swiss scientists and, when in Zürich in 1918, made the personal acquaintance of many more at a meeting of the Swiss Association. Again in Switzerland in 1920, he visited Dr. Schulthess expressly to discuss the possibility of holding the Third Congress there ; but it was generally agreed to be too soon. However, inquiries began to reach him in growing volume, an international congress on plant diseases was held in Holland in 1923 without incident, all the erstwhile warring nations having attended it, and so in the autumn of 1924, relying on Dr. Schulthess's known willingness to organise a Congress, Dr. Jordan circulated the members of the Committee. A spark that may have touched off action was a nine-page letter from the indefatigable Walther Horn suggesting that, because of the bitter aftermath of the war the two of them should organise an entirely new series of Congresses, ignoring the organisation set up at Brussels and Oxford. Horn's purpose was, apparently, in this way to avoid personal animosities that had developed within the Executive Committee. Wisely, Dr. Jordan rejected this proposal. The replies he received to his circular letter were somewhat mixed. Severin who now writes exclusively in French, replied (26th November, 1924) " réunir un congrès reservé aux seuls alliés et neutres ne me parait guère être un véritable Congrès et tôt ou tard on lui déniera toute importance sérieuse ". Lesne, though personally favouring the proposal, found himself unable to support it officially, and resigned. Other difficulties, too, arose. At Oxford Dr. Malcolm Burr had been General Secretary to the Executive Committee, but now, having had to give up entomology, he was no longer available. As at Oxford, so now, Dr. Jordan stepped into the breach. The correspondence he received as General Secretary is preserved, but, typewriters having apparently become unfashionable once more at Tring, the extent of his labours in replying to it all can only be guessed at, not assessed. During the first half of December, 1924, a number of entomologists in key positions throughout the world were informed that it had been decided to hold the Third Congress in Zürich in July, 1925—i.e. only seven months later! Walther Horn, whose entomological institute in Berlin was still in a pretty precarious state financially, owing to inflation, replies " Ich werde alles daran setzen, so viel Geld zusammen zu kratzen, dass ich nach Zürich komme ". Father Wasmann, in welcoming the decision, goes on to add a phrase that merits quotation, " the formidable war has obnubilated the idea of internationality of science . . . in many circles who pretend to be purely scientific! " However, eventually some 200 people arrived in Zürich and, as the published report of the Congress shows, held an enjoyable and profitable meeting, though it must be admitted that the effective value of many of the praiseworthy resolutions passed remains doubtful. As far as the continuity of the Congresses is concerned, one most important decision was taken ; Dr. Jordan was appointed formally Permanent Secretary of the International Congresses of Entomology. At the same time the old Permanent Committee, the usefulness of which had proved quite illusory, was abolished.

With the Zürich Congress ended Dr. Jordan might well have " sat back " for a while. Instead, he took his full share, with Walther Horn, of the burden of seeing the *Transactions* and *Proceedings* through the press, which was achieved almost within the year.

The Fourth Congress presented the Permanent Secretary with tasks of a quite different kind. This time it was not a question of finding a place and time to meet; that had been virtually settled at Zürich, and was finally decided by a resolution passed on 30th December, 1926, by the American Association of Economic Entomologists, which extended a cordial invitation to the Permanent (i.e. Executive) Committee of the International Entomological Congresses to hold the Fourth Congress in the third week of August, 1928, preferably at Ithaca. This resolution does not appear to have been formally considered by the Committee, but as it did little more than give formal effect to discussions that had gone on continuously between Dr. Jordan and Dr. L. O. Howard ever since Zürich, there was no need. Howard was then the acknowledged "king" of official entomology in the United States; what he proposed in such matters "went". A most efficient local committee was appointed and a highly successful Congress held.

During the preparations for this Fourth Congress the General Secretary was mainly preoccupied with two matters. First and foremost, how to ensure that a goodly representation of European entomologists reached Ithaca; secondly, to help and advise on many matters concerning the organisation of the Congress. Dr. W. J. Holland was particularly critical, in an entirely friendly way, of the set-up of the permanent organisation of the Congresses, and only after a voluminous correspondence was he finally satisfied—the bundle of papers referring to this Congress weighs over 22 lb.!

Many European entomologists are still sincerely grateful to Dr. Jordan for enabling them to pay a visit—all too brief for many of them—to the United States to attend this Congress. In 1927 he spent a month studying types of fleas in the U.S. National Museum, Washington. Clearly he did not confine himself to fleas; it was the application he made to the Carnegie Endowment for International Peace, with the active support of W. J. Holland and L. O. Howard, that won the day. The grant, as recorded in the *Proceedings* of this Congress paid the passages of 25 European entomologists, hardly one of whom would without it have been able to attend. Not content with this, Dr. Jordan raised other funds in England, organised the whole of the travelling arrangements for the European contingents, and contributed his own free passage to the common pool. The writer of this short article is among those who will always remember with gratitude his kindly, unhurried patience in gathering together and tending this flock. The Congress over, he straightway resumed his editorial burden. The *Transactions* and *Proceedings* of this Congress were edited once again by him and Walther Horn, and printed, not in the United States, but in Germany.

The next three Congresses—Paris, Madrid and Berlin—did not present Dr. Jordan with such a variety of difficulties to overcome as had the earlier ones, though involving him in plenty of work. The Ithaca Congress had decided in 1928 to accept the invitation from France so that the Fifth Congress could be held at the same time as the French Entomological Society celebrated its centenary, in 1932. Dr. Jeannel, already since 1925 a member of the Executive Committee, took over the General Secretaryship of the Paris Congress most efficiently. The Committee's files show that Dr. Jordan's main activities were organising the parties from the British Isles and trying to stimulate Governments, Ministries, Universities and Societies of all kinds throughout the Commonwealth and in the United States to send official delegates.

The latter was by far the larger task. Governments, particularly those of the larger powers, showed themselves rather reluctant to give formal recognition to the Congresses, though allowing themselves occasionally to be represented by officials from interested departments. At Oxford, according to the published *Proceedings*, only four governments had delegates, and even at Ithaca the number had only risen to ten, in spite of the fact that invitations had been sent out at governmental level by the State Department, Washington. At Paris, some twenty countries were represented by government delegates, and at Berlin forty-six. At the Madrid Congress, a smaller gathering than at Paris, there were eighteen. The Stockholm *Proceedings* give no list. The fact that at Amsterdam the number had fallen back to eighteen, probably reflects the increasing alarm of many governments at the rapidity of the proliferation of international congresses of all kinds.

The drafts and re-drafts of the report of the Executive Committee to the Paris Congress show that, up to the last minute, the Committee was in two minds as to whether to recommend Madrid or Berlin for the Sixth Congress. The former was chosen, but from then on nothing is recorded, or the papers are lost. This obscurity is peculiarly unfortunate because no record of the *Proceedings* of the Madrid Congress was ever published. Spain was in the throes of serious political trouble which manifested itself openly as civil war soon after the Congress, and it was only with great difficulty that the *Transactions* eventually were published. The Congress itself, though small by other standards, was one of the most enjoyable and productive. It was the last at which that meteoric entomologist Malcolm Burr attended.

The Seventh Congress, Berlin, 1938, had been highly efficient, thoroughly organised, liberally supplied with funds both for the event itself and for the publication of its *Proceedings* and *Transactions*. But it had somehow been an uncomfortable Congress. The strains and stresses of the political règime were evidently rocking the social structure of the people. In little more than a year they were to explode in another of the cataclysms that have bedevilled Franco-German relations and the political stability of Europe at intervals throughout the centuries. Many of those present doubted whether they would in fact meet again in three years' time. There were alternative possibilities also to be considered. Silvestri was anxious for the Congress to meet in Rome in 1942 when it was planned that a World Exhibition would be held in that young old city. However, after the Berlin Congress the Executive Committee received and accepted an invitation to hold the Eighth Congress in Stockholm in 1941 under the Presidency of Dr. Sjöstedt ; it also decided a congress should be held in the Netherlands in 1945, in conjunction with the centenary of the Dutch Entomological Society.

It was Trägårdh who took up the running immediately after the war. In a characteristically racy letter to Dr. Jordan in November, 1945, he expressed a hope that it was not necessary this time for thirteen years to elapse, even if the war had been a longer one, because " otherwise most of us will be gone, although entomologists are a hardy race ", . . . " assuming that the Congress will take place in 1952, the president Sjöstedt will be eighty-six and I, the vice-president 74 ". To this Dr. Jordan replied quickly that he was much in favour of Stockholm for obvious reasons, and the sooner the better, adding, no doubt with recollections of Zürich in mind, " it does not really matter how many countries are represented ; continuity of the Executive Committee and the Congresses is the main point ". Six months later (July, 1946) he is able to write that he has the agreement of half the Executive Committee and that this " with the President's vote decides the issue in favour of Stockholm in 1947 "—bringing forward Trägårdh's date by five years. " After you have decided the programme and date I shall write to prominent entomologists . . ." " Intelligent people are tired of being kept in closed compartments for political reasons. *Homo politicus* does not appear to me to be a desirable strain of *Homo sapiens* . . . other countries are so large their inhabitants do not get attacks of claustrophobia! " Gradually the threads are gathered together from Johannsen in America, Jeannel in Paris, Rimsky-Korsakow in Russia, and new names appear, Martin Hering in Berlin taking the place of the faithful Walther Horn, Vayssière, Chester Bradley and others. Having set the stage Dr. Jordan confidently leaves the play to Trägårdh and his able adjutants.

But another matter of considerable importance to the Congresses arose about this time. There had been in existence for many years an International Union of Biological Sciences which, prior to the war, had been mainly concerned with botanical matters. The advent of the United Nations and, in particular, of UNESCO revitalised this Union to such an extent that, realising its deficiencies in the zoological fields, and aided by funds from above, it set about creating international organisations in the various branches of zoological science comparable with those already existing in botany. By a fortunate chance it was to Dr. Jordan that I.U.B.S. addressed its first inquiries in respect of entomology, suggesting that the Executive Committee of the Congresses should become a Section of the Union, and baiting the hook with the statement that it was " planned that the Reports of the Congresses will be published by I.U.B.S. so that this large financial burden will be taken away from the International Congresses!" A disclaimer that this would have any adverse effect upon the independence of the Congresses was only natural. Eventually the Executive Committee recommended the Congress to accept this invitation, which it did, because, as Dr. Jordan remarked, it was better than setting up yet another international body. Thus the Executive (now Permanent) Committee of the Congresses is now also the Entomological Section of I.U.B.S. In the event too, it has preserved more than a little independence, the drying up of the source of supply having removed the threat of being bought out from above, though some valuable benefits have been received.

At Stockholm Dr. Jordan resigned from the Secretaryship of the Executive Committee, not from lack of interest but solely because his increasing deafness made it impossible for him to follow a discussion. His utterances at the meetings of the Committee in Stockholm had indeed at times somewhat embarrassed our Swedish hosts, for though very relevant to the general business they were not always entirely apposite to the immediate subject of discussion—neither was a funnel on the end of a length of flexible gas-tubing a very efficient hearing aid! Fittingly and with enthusiasm, at the final Plenary Session he was elected Honorary Life President of the Congresses and Life Member of the Permanent Committee. At Amsterdam, in 1951, the doyen of the party, his speech alone at the official luncheon was heard unaided throughout the great hall needed for the occasion. What of 1956 ?

What a change has come over the Congresses that Dr. Jordan founded.

What changes have we all seen whose lives span these fateful forty-five years. Through all this turmoil our unruffled Honorary Life President has held unfalteringly to his course, untrammelled by personalities or politics, gently turning aside the unwelcome, blandly ignoring what was best ignored, oblivious of rules, regulations or formalities that hindered progress, avoiding disputes in favour of sweet reason and the main issue, always courteous, friendly and infinitely patient. One last thought, perhaps may be allowed, for it is so entirely in keeping with the spirit of a man who still at the age of 93 looks only to the future. What of the future? Can our Congresses still go on? Will it remain practical to hold them? Are they becoming too expensive? Do they still serve any useful purpose ? So long as entomology is a living active force for good in the world, no doubt they will continue.

KARL JORDAN AND ZOOLOGICAL NOMENCLATURE.

By Francis Hemming

(*Secretary to the International Commission on Zoological Nomenclature.*)

Dr. Karl Jordan, after having served as an Alternate Member of the Commission at the memorable Session held at Monaco in 1913 during the Ninth International Congress of Zoology, was elected a full member of the Commission as from the close of that Session, and was placed in Class 1922 in succession to Professor Karl Apstein of Berlin, who was then transferred to the Class 1919 in place of Professor K. Krapelin of Hamburg, resigned. In February, 1922, Dr. Jordan was elected President of the Commission in succession to the late Professor F. S. Monticelli of Naples. Dr. Jordan held the office of President for just over nineteen years, retiring at his own request on account of his age at the session of the Commission held in Paris in July, 1948. During this period Dr. Jordan, who had long been an outstanding figure in the zoological world, won not only the esteem but also the warm affection and regard of the many zoologists in all parts of the world with whom his high office brought him into close contact. Dr. Jordan's decision to vacate the Presidency was received with the greatest regret by the zoologists attending the Paris Congress, by which he was unanimously elected Honorary Life President of the Commission. At the same time he was persuaded to retain his post as a member of the Commission until such time as his successor was fully established in office. Dr. Jordan finally resigned his membership of the Commission in May, 1950, when he was succeeded by his friend and colleague Mr. N. D. Riley, of the British Museum (Natural History).

The situation as regards the international regulation of zoological nomenclature was one of extreme delicacy at the time when Dr. Jordan was first called to the membership of the International Commission. The *Règles Internationaux* had been adopted by the Fifth International Congress at Berlin in 1901 with the greatest difficulty owing to the long established diversity of practice among zoologists in the field of nomenclature resulting in the complete absence till then of a set of international rules. There was general agreement that the adoption of an international code was long overdue, but the greatest difficulty was experienced in securing agreement on the more fundamental of the issues involved. This project was first raised in a serious fashion at the First International Congress of Zoology held at Paris in 1889, when Professor Raphael Blanchard, the eminent French zoologist who acted as Secretary-General of that Congress, put forward a draft set of rules for consideration. The Blanchard draft did not succeed in securing general agreement and it was for this reason that in 1895 the Third International Congress at Leiden established the International Commission on Zoological Nomenclature to study all existing unofficial sets of rules and to submit proposals to the next Congress. The report submitted by the Commission to the Fourth International Congress held in Cambridge in 1898 also failed to secure agreement, that Congress referring the matter back to the Commission for further consideration. When, therefore, the Berlin Congress met in 1901 it seemed evident that, if an international set of rules was ever to be secured, it was essential that agreement should be reached at that meeting. During the twelve years during which the project had been under discussion, substantial progress had been made on many matters, but there was still no real agreement on a number of the more fundamental issues. The more conservative-minded zoologists were in a substantial majority at the Berlin Congress and it was evident that they were determined that either the Law of Priority should figure in the rules in its most rigorous form or that there should be no international rules at all. Those zoologists who were equally anxious that a set of international rules should be adopted by the Congress but who desired that priority should be tempered by mercy bowed to the force of circumstances. In consequence, the *Règles*, as adopted by that Congress, set out in Article 25 the Law of Priority in its most unqualified form. The Berlin Code was not published until 1905 and, as was only natural, it was several years after that date before individual specialists made serious attempts to apply its provisions to the nomenclature of their groups.

By the time that the Commission and the Congress met at Graz in 1910 it had become evident that, if the Berlin rules regarding Priority were to be ruthlessly applied, large numbers of names which were household words to every zoologist would either disappear in synonymy or, even worse, would need in future to be used in some entirely different sense. At the Graz meeting both the Commission and the Congress sought to find palliatives by the proposed adoption, for example, of an Official List of Approved Names, the object being to show that, even if many well-known names would go by the board under the Berlin Code, there would still be many others left unscathed. Feeling against the rigours of the Law of Priority ran very strong at Graz, so much so that the palliatives then put forward by the Commission were swept aside as inadequate. It is not surprising therefore that, when three years later the Commission and the Congress met at Monaco in 1913, the situation was one of great delicacy. At that time the Commission was still composed in the main of veteran zoologists who had spent their working life untrammelled by any rules at all and who were for the most part firmly of the opinion that only by the unqualified acceptance of the Law of Priority could stability in nomenclature ultimately be achieved. All the signs suggested therefore that the Commission would find itself in irreconcilable opposition to the younger zoologists who formed the main membership of the Congress, and who were determined that the nomenclature of their particular groups should not be wrecked by a policy which at the most could only claim that on the ruins so created zoologists of later generations would be able to secure a stable nomenclature.

The Monaco Session of the International Commission was the first at which vacant seats at its table were filled for the duration of the Congress by the appointment of Alternate Commissioners. The two zoologists who thus became Alternate Commissioners at this memorable session were the late Lord Rothschild and Dr. Karl Jordan. While the surviving records of the Commission of that date are of the most meagre description and those which do survive show a not unnatural reticence in describing the events of the Monaco session, it is clear that the powerful combination represented by the two alternate Commissioners at once excercised an influence upon the course of the deliberations of the Commission. During that meeting the Commission agreed without difficulty upon a proposal that the Congress should establish an " Official List of Generic Names in Zoology " and that the Commission should be charged with the responsibility for maintaining and developing this instrument for the promotion and stability in nomenclature. On the central issue of priority versus stability, however, it seemed up to the last moment that the older members of the Commission had succeeded in imposing their view upon their younger colleagues. When however, the Commission held its customary joint session with the Section on Nomenclature of the Congress, it was confronted with such a spirit of hostility that it became clear either that the Commission would have to bend to the storm or be swept away. It was at this critical stage that the young Alternate Commissioner, Dr. Jordan, stongly backed by his powerful chief Lord Rothschild, succeeded in infusing a spirit of reason into the hurried meetings of the Commission which then took place. As a result the Commission, though still not unanimous, came back to the Congress with a proposal that it should be given Plenary Powers to suspend the normal operation of the *Règles* in the interests of nomenclatorial stability when, in its opinion, the strict enforcement of those *Règles* would clearly result in greater confusion than uniformity. This proposal won the support of the Section on Nomenclature and was endorsed by the Congress at its final plenary session. For this act of zoological statesmanship it is to Dr. Jordan more than to any other man that later generations of zoologists are indebted.

The outbreak of war in Europe in 1914, coming so soon after the close of the Monaco Congress, was a severe set-back to the international regulation of zoological nomenclature. Not only were many zoologists diverted to war work from their normal studies, but in addition the break so caused robbed the decisions taken at Monaco of much of their practical value. In consequence for many years after the war little progress was made either with the building-up of the *Official List of Generic Names in Zoology*, or with the grant of relief by the Commission in particular cases through the use of its Plenary Powers. The earlier part of the inter-war period was marked in the field of zoological nomenclature by a spirit of disillusionment and, as far as the International Commission was concerned, by one of defeatism. It seemed as though it had forgotten the lessons which it had learned at Monaco and in its general approach to zoological nomenclatorial problems it reverted to the rigid adherence to the Law of Priority which had brought it into such violent collision with the general body of zoologists at the last Congress held before the outbreak of the war. The situation was therefore one of great difficulty when in 1922 Dr. Jordan was called upon to assume the Presidency of the Commission. In the general climate of that time it was not possible for him to set the Commission on a new course as far as concerned the major issue of principle which still divided that body from zoologists generally. In other respects, however, the new President quickly made his influence felt on the general work of the Commission. In particular, under his influence substantial progress was made both in disposing of old cases submitted to the Commission for decision and in expediting the consideration of new cases. The success achieved by President Jordan in this field is illustrated by the fact that between the years 1924 and 1930 the number of cases dealt with by the Commission in the form of *Opinions* rendered showed an increase of over 50 per cent. as compared with the period prior to his election as President. During these years Dr. Jordan, by the skill and tact with which he guided the difficult body of which he was the President, enormously increased his prestige and authority. It was well for the Commission that he did so, for when in 1930 the Commission assembled at Padua at the meeting of the Eleventh International Congress of Zoology it was called upon to face a crisis even more severe than that through which it had emerged with such difficulty at Monaco in 1913. Although at that Congress a break had been made in the deadlock created by the extreme rigidity of the provisions relating to the Law of Priority adopted at Berlin in 1901, no attempt had been made to grapple with the other major problem arising out of the application of the Berlin Code which then divided zoologists. This controversy was concerned with the meaning to be attached to the expression " nomenclature binaire " (binary nomenclature), as used in Proviso (b) of Article 25. The question at issue was whether or not to accept as available names, generic names published by authors who while recognising that the scientific name for an animal must be so constituted as to denote the two-fold concept of genus and species, nevertheless had not applied the binominal system to nomenclature. Unfortunately in this field also the Commission by a decision taken in *Opinion* 20 (relating to the status of generic names published in the *Zoophylacium Gronovianum* of Gronovius) had set itself in opposition to the general wishes of zoologists. For in that *Opinion* it had given a ruling that generic names published by non-binominal authors who adopted the so-called " binary " system of nomenclature were to be accepted as possessing the status of availability under Article 25. Repeated efforts were made during the twenties to persuade the Commission to revise the unfortunate decision which it had taken in this matter. The Commission, however, refused to modify its position, the majority of its members being either convinced that the decision in *Opinion* 20 was the correct decision, or unwilling publicly to recognise that a mistake had been made.

At the Padua Congress the resentment felt by zoologists on this subject suddenly came to a head. At the Budapest Congress of 1927 the Commission had taken the view that this matter was not open to discussion since the ruling given in *Opinion* 20 was, it was claimed, the formal expression of a " gentleman's agreement " entered into at the time of the adoption of the *Règles* at Berlin twenty-six years earlier. At Padua the Commission, though divided internally on this matter, was still of the same opinion as a body. It was therefore totally unprepared to meet the situation which developed when, at the joint meeting of the Commission and the Section on Nomenclature of the Padua Congress, Dr. Walther Horn of Berlin brought forward without preliminary notice a resolution asking the Congress in Plenary Session to re-interpret Article 25 of the *Règles* in such a way as to make it clear that names published by non-binominal but so called " binary " authors did not satisfy the requirements of that Article. No doubt if Dr. Jordan had thought it in the general interest he could, as President of the Commission, have prevented Dr. Horn's resolution from being brought to a vote, in view of the irregularity of the manner in which that resolution had been brought forward. With a courage and long-sightedness which later were to prove to have been fully justified Dr. Jordan, however, decided not to intervene in this way, and he thus made possible a direct expression by the Congress of its views on this subject. Accordingly, after an extremely acrimonious discussion the so-called " Horn Resolution " was adopted by the Section on Nomenclature by a majority and was later endorsed by the Padua Congress in plenary session.

The period immediately following the explosion at Padua was naturally one of great confusion and difficulty. Those members of the Commission who had voted in the minority were deeply affronted by the action taken by the Congress, so much so indeed that there were those among them who doubted the utility of maintaining the Commission in existence. It was in these years that Dr. Jordan's capacity for leadership and his skill in dealing with men proved of the greatest possible advantage. To him must be given the credit for the change of spirit on this subject shown by the Commission when it met at Lisbon in 1935. It was evident to everyone that means must be found for preventing the recurrence at this and subsequent Congresses of violent disputes such as those which had occurred at Padua, for such disputes were not only highly injurious to the International Commission as a body, but also open to the strongest objection from the point of view of the authorities of the Congress. Immediately upon his arrival at Lisbon, Dr. Jordan entered into discussions on the subject with M. Maurice Caullery, the eminent French zoologist who was the President of the Comité International Permanent des Congrès de Zoologie, with a view to devising a solution which, while saving the face of the Commission, would at the same time pave the way to the acceptance by a later Congress in an orderly fashion of the substance of the reform sought in the resolution moved at Padua by Dr. Horn. This discussion led to an agreement between Dr. Jordan and M. Caullery. M. Caullery for his part undertook to advise the Comité Permanent to refer back to Dr. Jordan, as President of the Section on Nomenclature, the subject matter of the so-called " Horn Resolution " adopted by the Eleventh (Padua) Congress, with a request that the Section should examine this matter in detail before the next following Congress and submit to that body a comprehensive report with recommendations designed to settle this long protracted controversy. Dr. Jordan, for his part, undertook to endeavour by all means at his disposal to persuade the Commission to accept such a recommendation if proposed to it by the Section on Nomenclature. During the Congress, the Comité Permanent adopted a resolution in the sense recommended by M. Caullery, its president, and the way was thus cleared for Dr. Jordan to place this matter before the International Commission. This Dr. Jordan did at the fifth meeting of the Commission during its Lisbon Session, held on Wednesday, 18th September, 1935. The task was one of great delicacy, for though under Dr. Jordan's leadership there had been a change of heart in the Commission, the painful impression created by the Padua debates still lingered in the minds of some of the members of the Commission. Dr. Jordan, in bringing forward his proposal, not only urged the essential reasonableness of the course proposed, but also brought into play all his powers of persuasion to win over those members of the Commission to whom the action proposed was personally distasteful. In this matter he was strongly supported by his old friend and colleague Dr. Leonhard Stejneger, the senior U.S. Commissioner present at the meeting. At the close of this discussion the Commission agreed unanimously to accept the invitation addressed to it by the Section on Nomenclature on the initiative of the Comité Permanent. Thus it was that Dr. Jordan set the Commission on a path which was to enable it in Paris in 1948 unanimously to submit to the Congress a report clarifying the meaning of Article 25 in the sense which had been advocated by Dr. Horn at Padua eighteen years earlier.

In quite another field also the session held by the Commission at Lisbon in 1935 brought new problems to be dealt with by Dr. Jordan as its President.

For it was at that session that the Commission received from the late Dr. Charles Wardell Stiles a letter intimating his desire on account of age and infirmity to be released from the duties of the office of Secretary, an office which he had held continuously for nearly forty years. The vacancy in the secretaryship so created was not filled at the Lisbon session, but under Dr. Jordan's guidance the Commission then took a series of decisions on the arrangements to be made for the continuance of its work after the retirement of Dr. Stiles. In the administrative field the problem was one of great difficulty, for the Commission at that time possessed no funds of its own and it was evident that it would be no easy matter either to secure the funds needed to enable the Commission to continue its work, or to devise the administrative mechanism required for that purpose. Ultimately the Commission decided to confer upon the President and the new Secretary of the Commission when elected, plenary power to take all necessary action to establish the secretariat of the Commission at its new headquarters, to secure the publication of the *Opinions* of the Commission from time to time, to obtain the finance required for the due functioning of the Commission and generally to secure the effective continuance of its work. Following the election in 1936 of myself as Secretary in succession to Dr. Stiles, the headquarters of the Commission were transferred to London and the first task of Dr. Jordan and myself was to obtain at least sufficient funds to enable the work of the Commission to be re-started. Dr. Jordan at once addressed himself to this problem and by the beginning of 1939 a fund of about £300 had been secured through gifts received from the Royal Society, the British Museum (Natural History), the British Association for the Advancement of Science and the Zoological, Linnean, and Royal Entomological Societies of London. Dr. Jordan then judged that the stage had been reached at which decisions could usefully be taken on all matters necessary for the effective re-starting of the work of the Commission. These problems formed the subject of consideration at a Plenary Conference held in London between Dr. Jordan and myself on 19th June, 1939. At this Conference a long series of decisions was taken with regard to the future form of organisation to be adopted for the office of the Commission. In addition it was decided that, despite the tenuous character of the financial resources available, the Commission should assume direct responsibility for the publication of its own *Opinions*. Under this decision the first *Opinions* of the new series (*Opinions* 134–136) were published at the end of August, 1939.

The outbreak of war in Europe a few days later created a situation of the greatest difficulty for the Commission. These difficulties served, however, only to provide Dr. Jordan with a further opportunity of displaying in the administrative field talents equal in distinction to the contributions in the field of zoological nomenclature which he had already made at Monaco in 1913 and still more at Lisbon in 1935. For it was by the vigorous measures which Dr. Jordan then adopted that he succeeded in bringing the Commission through the War not only intact, but greatly strengthened in many ways. The anxieties felt in September 1939 by Dr. Jordan as President and by myself as Secretary arose not merely from the fact that it was impossible to forecast how long the war then starting would continue, but also because of the risk that, in consequence of the development of the air arm and the prospect of air-raids on centres of population, either or both of the principal officers of the Commission might become casualties in air-raids or the records of the Commission might be destroyed. As a first step Dr. Jordan, as President executed an " Emergency Powers Declaration " under which as President he assumed powers for the duration of the emergency to renew the Classes in the Membership of the Commission when these became time-expired, and to fill the offices of the Commission if any of these became vacant through the expiry of the term of service of the Classes of which the officers concerned were members. Finally, under the same " Declaration " Dr. Jordan assumed powers to issue Directions providing in advance for the management of the affairs of the Commission in the event either of him or me becoming a war casualty. From time to time during the war Dr. Jordan issued Directions under the Emergency Powers Declaration, with the result that at the end of the war the Commission emerged with its membership unimpaired.

All during these difficult years Dr. Jordan also played a determining part in the remarkable progress achieved in the work of the Commission notwithstanding the extraordinary obstacles of the day. The decision taken by the Plenary Conference in June, 1939, that the Commission should itself publish its *Opinions* was vigorously pursued. In consequence, by the end of the war forty-eight *Opinions* (*Opinions* 134–181) had been rendered and published, these *Opinions* embodying the decisions on individual problems taken by the Commission during its Lisbon session. In addition a new series, styled " Declarations ", was instituted for recording resolutions adopted by the Commission in regard to more general matters. During the same period nine such *Declarations* embodying resolutions adopted by the Commission at the Monaco (1913), the Budapest (1927) and the Padua (1930) Congresses were rendered and published together with three further *Declarations* embodying similar resolutions adopted at Lisbon in 1935.

Finally in 1942, Dr. Jordan gave his consent to the adoption of the project for the establishment on behalf of the Commission of a serial publication in which would be published all applications submitted to the Commission for consideration, thus providing the means to zoologists at large to express their views on cases submitted to the Commission before decisions were taken thereon. This led to the publication in May, 1943, of the first part of the *Bulletin of Zoological Nomenclature*.

By these means Dr. Jordan piloted the Commission safely through the crisis created by the war, and in addition provided it with new mechanisms for the better discharge of its duties. It was natural therefore that at the close of the war he should seek to be relieved of the burdens of the office of President. Dr. Jordan had added greatly to the lustre of the Presidency during his distinguished tenure of that office and for this reason and because also of his age, his colleagues felt unable to resist his request that he might be permitted to transfer his duties to younger hands. In his letter of farewell to the Commission Dr. Jordan struck a note which was highly characteristic of the manner in which he had always viewed the subject of zoological nomenclature, for, while recognising its importance in its own field, he had always been at pains to make it clear that he regarded it as no more than a working tool to be placed in the hands of zoologists. At the same time he pointed with justifiable pride to the fact that the Commission represented a form of international co-operation which had come unscathed through the unparalleled political discords of the preceding years. It seems fitting to close this note on Dr. Jordan's services to the International Commission and to zoological nomenclature generally by quoting the following passage from his last letter to the Commission :

" One or other of the Commissioners may at times be inclined to regret the hours spent on the consideration of nomenclatorial questions which do not directly concern his own field of study ; but the thought should ever be present in our minds that nomenclature is an international language and the only international undertaking on the basic principle of which all biologists agree ; the same name for the same animal in science throughout the globe. I know that there are highly intelligent biologists who look upon nomenclature with disdain because the great fact has escaped them, that in the present spiritual turmoil in which humanity finds itself one point of general agreement, like the basic principle of nomenclature, renders general agreement in other matters a possibility and gives humanity some hope."

KARL JORDAN'S STUDIES ON SIPHONAPTERA.

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Dr. Karl Jordan's contributions to our knowledge of the Order Siphonaptera have been so numerous and so outstanding that specialists of the study of fleas find it difficult to comprehend that Dr. Jordan is simultaneously an international authority on Lepidoptera, on anthribid beetles and various other groups of insects, as well as on natural history in general. In fact, the volume and calibre of Jordan's researches on Siphonaptera are such that one scarcely knows where to begin an appreciative essay, unless it is to state that only after re-studying Jordan's papers does one fully recognise one's own shortcomings—and realise the magnitude of the debts we owe to the Dean of Siphonapterists. I feel obliged to point out at the onset that it is difficult to be objective in this essay because, in addition to having the highest respect for Dr. Jordan as a scientist, I have an extremely warm affection for him.

In order fully to appreciate Jordan's researches on Siphonaptera, it is necessary to realise that this order of insects, although very small, includes a great number of tremendously diverse forms, there being about 225 generic names to encompass a mere 1400 known species and subspecies. The various paths of evolutionary development, coupled with the extinction of many fleas that died with hosts now known only as fossils, have frequently resulted in monotypic genera, and, in fact, a single species may be all that is known of a distinctive tribe or subfamily! It is axiomatic that the affinities of such species are enormously difficult to determine, particularly since the phenomena of adaptation and convergence have further obscured the relationships. Authors, basing their views upon small and unrepresentative collections, have frequently been led astray for these reasons. The outstanding exception throughout the history of the study of fleas has been Karl Jordan. We have been indeed fortunate that this eminently qualified zoologist and taxonomist chose to work on fleas (although as a sideline or hobby) and that he had access to the world's largest and most representative collection of Siphonaptera. After fifty years' study of fleas, undertaken despite a multitude of other interests and duties, this interest in an aberrant, difficult and little studied group culminated in a concept of systematics which is so sound that new and strange genera and species that are still being collected in remote areas can be smoothly fitted into their proper slots.

Jordan first became interested in fleas as long ago as 1898 (5), when he encouraged N. C. Rothschild's scientific bent towards a study of these insects at that time. However, since he was primarily a coleopterist and lepidopterist, Jordan at first remained much in the background, although preparing the illustrations for Rothschild's papers and doubtlessly otherwise influencing much of Rothschild's work. The astonishing maturity of the first major opus bearing his name, the 1906 Revision of Sarcopsyllidae (with N. C. R.), makes it evident that he had already acquired a sound background in the subject. While another fine revision by the two authors appeared shortly thereafter (26), and many excellent joint papers followed, Jordan evidently considered the study of fleas a purely secondary mission, to be wedged in among researches on Lepidoptera, Coleoptera, Hemiptera and other subjects. Prior to 1925, his name as sole author appeared only on three papers on fleas, but after the initial shock of the profound loss occasioned by Charles Rothschild's death, Jordan intensified his investigations on the subject. Descriptions of new species and genera poured forth until the onset of the second World War, when he began a series of papers on evolutionary developments and relationships within the order, interspersed with descriptive papers of customary excellence.

Certain characteristics of Jordan's work are at once apparent even to those beginning the study of Siphonaptera. The first impression is that of prodigious output, far exceeding that of any other worker, even though his prime mission at the Tring Museum was concerned with other groups of insects, and even though he was simultaneously active with the International Entomological Congresses, the International Commission on Zoological Nomenclature, and served as Director of the Museum.

The astonishing productivity of Jordan in this field is shown by the following table, which is based upon available records and which may not necessarily be complete :

TABLE I.—*Articles on Fleas by Dr. Jordan.*

Author.	Articles.	Pages.	Figures drawn by Dr. Jordan.	New genera.	New species.	New Sub-species.
Jordan . . .	**103**	**787**	**772**	**49**	**208**	**74**
Jordan and Rothschild	**38**	**683**	**511**	**26**	**171**	**27**

It should be borne in mind that practically all of the 375 illustrations in N. C. Rothschild's papers on fleas were also prepared by Jordan. Further, there was only one assistant to help sort, prepare and mount the thousands of specimens utilised in these studies. Jordan not only did much of this work himself, but also personally typed and edited the manuscripts, and took care of his voluminous global correspondence.

Impressive as these statistics are, their significance does not lie in mere volume alone, but rather in the uniformly superior quality of the work performed. For example, there are disproportionately few synonyms in this tally. Those that have occurred have almost invariably been due to the fact that other workers were simultaneously studying and describing fleas without Jordan being aware of the species involved. Another reason was due to the lack of correct association of the sexes. That so many of these genera, species and subspecies are valid cannot be simply ascribed to the fact that Jordan operated at a time when fleas were yet largely undescribed. Some workers antedating Jordan, as well as certain more current contemporaries, managed to create goodly numbers of synonyms while describing fleas.

When Jordan did err, it was almost wholly inevitable, particularly when reconsidered in the light of how little was then known about siphonapteran morphological variations, and, more especially, about the geographical range of certain fleas. Only within the last few years has it been appreciated that some fleas, formerly believed to have been restricted to one area, have an extremely broad range. Our current knowledge is so different from that of a few years ago that this point is worthy of further discussion and illustration. For example, *Polygenis roberti* Rothschild, 1905, described from southern Brazil, is now known to range to northern Venezuela (36) and even to Guatemala. *Dasypsyllus gallinulae* (Dale, 1878), a flea well known as a parasite of certain birds in the northern regions of the Old and New Worlds, has been found in the mountains of Panama (35) and the Philippines (32). It is clear that the creation of synonyms under such conditions is unavoidable.

The student of Siphonaptera is immediately impressed with the clarity of Jordan's taxonomic descriptions, particularly when he tries to prepare some of his own. Jordan's descriptions invariably have been terse, concise, simple but nevertheless clear and accurate. The characters employed have regularly been critical and significant ones, even though Jordan may have pioneered in their use. Another habit for which he has repeatedly been blessed was that of consistently comparing a new form with a close relative, and indicating pertinent similarities and differences. It is difficult to overemphasise the tremendous value of the illustrations Jordan prepared to supplement his descriptions, since he consistently was in advance of his contemporaries in the number of figures drawn and in their accuracy and scope. Jordan drew no unnecessary lines, and his figures have always been of a very high standard, with the essential taxonomic features clearly portrayed. Several instances come to mind of having collected a strange flea which turned out to be something unreported since originally described by Jordan or Jordan and Rothschild thirty or forty years ago. The species were nevertheless instantly and unmistakably recognisable by the illustration, if not by the description. Morphological structures not previously mentioned in descriptions were often illustrated, and colleagues have frequently been surprised to find that a " new " character had already been well illustrated by Jordan years ago. For example, Jordan not infrequently drew figures of various structures of the phallosome, adequately illustrating features which were not homologised or appreciated until a much later date. He was also the first scientist really to utilise phallosomal structures (other than the " paramere") for taxonomic purposes, and his study of the phallosome in *Rhopalopsyllus s. lat.* (15) is a classic.

It is also important to note that from the beginning Jordan had a species concept that is still in accord with the most modern views, and that he pioneered in establishing such a concept. It is difficult to recall an instance in which one of his species is now considered a subspecies or vice versa. He was also far ahead of his contemporaries as concerns a generic concept. Jordan, or Jordan and Rothschild, were instrumental in logically revising such catch-alls as *Pulex*, *Ceratopsylla* and *Typhlopsylla*. The names or concepts they proposed or utilised for the groups of fleas within these and other dust-bins still stand. Jordan described genera particularly carefully, and as a result virtually all his genera are valid today. We are fortunate that he was so conservative regarding what he considered to be of generic level, because the specialist in the field can cite too many non-Jordan genera whose current status is in real doubt and instances where familiar names suddenly appeared under aliases. Jordan reluctantly undertook to rèvise the American *Ceratophyllus* only after the splitting-up had already begun and there was " no means of stopping the process of dissolution from going on " (11). He went on to state " If I here inflict on science a number of new generic names, I plead the excuse that the divisions of *Ceratophyllus* I here define would inevitably be named by somebody else, probably by someone who does not know these fleas, as has happened in other orders of insects."

It is sometimes possible in entomology to guess the author of a new scientific name merely by the type of name employed. This can often be done with Jordan's names, and in this case the statement is meant as a true compliment, for his *nomina* have nearly always been euphonious, precise, and often short yet highly descriptive. Thus, *Opisocrostis* is indeed tassel-tailed, *phoberus* formidable and *rugatus* wrinkled.

Of course the name Karl Jordan and the modern geographical definition of a subspecies are virtually synonymous, and Mayr (29) has referred to "the most useful of all the working hypotheses in taxonomy, that of geographic representation". Jordan and Rothschild were naming truly geographical races of fleas as far back as 1912, although Rothschild (30) and Wagner (38) both named varietal forms in 1898 in the older sense of minor morphological variation.

Taxonomic research is sometimes belittled as merely indicating differences between groups of animals. Jordan's studies indicate how false is this view, at least insofar as concerns the sound systematist. Indeed some of Jordan's most profound discoveries in the field deal with the *resemblances* between certain groups of fleas and in discovering which morphological features are basic, phylogenetic, and which are merely adaptive, i.e. specialisations, or modifications, demonstrating convergence, parallelism, or reduction. Thus, notes on the affinities of groups of species or of genera, available nowhere else, are often included along with the description, as in the following highly significant passage. "*Neotyphloceras* have very complicated male organs and are related most closely to *Chiliopsylla*; they belong to the Ctenophthalminae and are distinguished from all other members of that subfamily by the fact that the anterior corner of the prosternum projects forward over the base of the anterior coxa (22)". Dr. Jordan noted that in virtually all fleas, on the mid and hind femur, the outer of the paired apical bristles is the shorter, whereas on the fore-femur almost invariably the outer bristle is the longer (20).

Among the many important concepts about the classification, relationships, distribution and host-relationships of fleas which were first advanced by Jordan may be mentioned the following: Bird-fleas are invariably closely related to and apparently derived from fleas which normally parasitize rodents. Such fleas have thus been secondarily adapted to birds. Further, although fleas of non-related genera may parasitise birds, if they possess a pronotal comb of spines, they always have a significantly greater number of spines in this comb than do their near relatives from mammals.

Jordan's remarkable powers of observation and perspicacity in detecting resemblances as well as differences are indicated by the note that only *Idiochaetis* Jordan, 1937, and *Thaumapsylla* Rothschild, 1907, which are in two separate families, have a semi-transparent line on the thorax, between the comb and the row of long bristles (20). This is believed to be fundamental. Jordan also called attention to the fact that the fracticipit condition of the head was correlated with the presence of vertical combs on the head and with that of false combs on the tibia. He further pointed out that these three conditions occur together in some Pygiopsyllidae, as well as in other families. Another pertinent noteworthy finding was that in the bat flea *Thaumapsylla breviceps* Rothschild, 1907, the

TABLE II.—*Systematic position of certain genera of Siphonaptera according to various authors.*

	CERATOPHYLLIDAE										HYSTRICHOPSYLLIDAE											PULICIDAE			LEPTOPSYLLIDAE
	ACERATOPHYLLINAE	ANOMIOPSYLLINAE	CERATOPHYLLINAE	CTENOPHTHALMINAE	LEPTOPSYLLINAE	NEOPSYLLINAE	RHADINOPSYLLINAE	UROPSYLLINAE	VERMIPSYLLINAE	(UNSPECIFIED)	ANOMIOPSYLLINAE	CTENOPHTHALMINAE	DINOPSYLLINAE	LEPTOPSYLLINAE	HYPSOPHTHALMINAE	HYSTRICHOPSYLLINAE	NEARCTOPSYLLINAE	NEOPSYLLINAE	RHADINOPSYLLINAE	STENISTOMERINAE	(UNSPECIFIED).	" SPILOPSYLLINAE "	ANOMIOPSYLLINAE	(UNSPECIFIED)	(NEAR CERATOPHYLLIDS)
LEPTOPSYLLA J. & R.					HOLLAND TRAUB+(31)									WAGNER J. & G. E. & F. C. & H.							EWING HUBBARD				**JORDAN(21) TRAUB (33) H. & R.**
CTENOPHTHALMUS KOL.				EWING WAGNER J. & G.								**E. & F. JORDAN HOLLAND H. & R.**						C. & H.			HUBBARD TRAUB				
PHALACROPSYLLA ROTHS.						WAGNER				EWING HUBBARD						E. & F. C. & H.		**J. & G. JORDAN (21) HOLLAND TRAUB*(31) H. & R.**							
CATALLAGIA ROTHS.			EWING E. & F. C. & H.			WAGNER												**J. & G. JORDAN (21) HOLLAND TRAUB*(31) H. & R.**			JORDAN(13) HUBBARD				
NEOPSYLLA WAGNER						WAGNER						E. & F.						**J. & G. C. & H. JORDAN (21) HOLLAND TRAUB*(31) H. & R.**			EWING JORDAN(13) HUBBARD				
NEARCTOPSYLLA ROTHS.														J. & G E. & H. C. & H.	WAGNER		HOLLAND		**JORDAN (21) TRAUB (34) HOPKINS (4) H. & R.**		EWING HUBBARD				
CORYPSYLLA C FOX														J. & G. E. & F. C. & H.	WAGNER		HOLLAND		**JORDAN (21) TRAUB (34) HOPKINS (4) H. & R.**		EWING HUBBARD				
PARATYPHLOCERAS EWING												E. & F.						C. & H.	**JORDAN TRAUB H. & R.**		HUBBARD				
TRICHOPSYLLOIDES EWING							J. & G.		E. & F. C. & H.										**JORDAN*(14-21) HOLLAND TRAUB (34) H. & R.**		HUBBARD				
RHADINOPSYLLA J. & R.							WAGNER J. & G.			EWING		E. & F.						C. & H.	**JORDAN (21) HOLLAND HOPKINS (4) TRAUB (34) H. & R.**		HUBBARD				
ANOMIOPSYLLUS BAKER	WAGNER	J. & G.									**J. & R.* HOLLAND T. & T. H. & R.**											E. & F.	C. & H.	EWING HUBBARD	
MEGARTHROGLOSSUS J. & R.	WAGNER	J. & G.									**J. & R.* HOLLAND T. & T. H. & R.**										HUBBARD	E. & F.	C. & H.	EWING	
CONORHINOPSYLLA STEWART	WAGNER		J. & G.					E. & F.			**JORDAN*(12) HOLLAND T. & T. H. & R.**										HUBBARD		C. & H.		
CALLISTOPSYLLUS J. & R.	WAGNER	J. & G.									**J. & R.* HOLLAND T. & T. H. & R.**										HUBBARD	E. & F.	C. & H.	EWING	
STENISTOMERA ROTHS.			E. & F.								**J. & R.* HOLLAND T. & T. H. & R.**		WAGNER	J. & G.						C. & H.	EWING HUBBARD				

Explanation of symbols : □, Correct position according to consensus of current concepts. *, By stated affinity. +, By obvious intent. E. & F., Ewing and Fox, 19
H. & R., Hopkins and Rothschild, 1953. C. & H., da Costa Lima and Hathaway, 1946. J. & G., Jellison and Good, 1942. J. & R., Jordan and Rothschild, 1915. T. & T., Tr
and Tipton, 1951. Numbers in ( ) refer to Bibliography.

alternate or intercalary bristles on the postantennal region of the head are large instead of being small as is typically (if not always) the case. This suggested to Jordan that the 3-toothed condition of *T. dina* Jordan, 1937, is a primitive character, and that bat fleas originally had more teeth in the head comb than the two found in all bat fleas other than *T. dina* (19).

It was while making such remarks that Jordan made the following dictum: " This sporadic distribution of a definite characteristic is the rule, rather than the exception in fleas. This fact is of great taxonomic significance, apparently much obscuring classification, but in reality clearing away preconceived ideas of near relationships. The early opinion that the presence or absence of the eye or of this and that comb were of primary importance in classification has been found erroneous long ago, but other similarly arbitrary notions have persisted (20) ". This quotation merits further discussion, particularly as regards its background.

As early as 1908 Jordan and Rothschild realised that superficialities were being considered fundamental in the current classification of fleas. Although their revision dealt with " non-combed eyed Siphonaptera," they clearly showed that fleas which were not related fell into this arbitrary category, while some close relatives were excluded.

While recognising the importance of describing new genera and species, Jordan appreciated the need for studies of a revisionary nature, and some of the earliest major works in this field bear his name, dating from 1906. One of his finest efforts of this type was his 1926 paper on *Xenopsylla* and Allied Genera of Siphonaptera (9), which clearly was taxonomically far ahead of contemporary articles by other authors. In addition to making it possible for the first time for workers on fleas readily to determine known species of *Xenopsylla*, this paper contains noteworthy examples of convergence. Thus, it was pointed out that well-developed genal lobes and occipital tubers occur in non-related pulicids. Jordan also made the interesting observation that pulicids occurring on birds differ from those on mammals regarding the arrangement of the tarsal plantar bristles.

In 1945 he showed that the presence or absence of the frontal tubercle is often of little value as a taxonomic character, particularly since the tubercle is deciduous in some instances (18). He was too polite to point out that another worker had described a generic synonym because he was misled by the deciduous character of the tubercle in *Sternopsylla* C. Fox, 1914.

Unlike certain other workers, Jordan consistently grouped fleas on the basis of characteristics which have proved to be fundamental, instead of such features as the presence or absence of an eye or of the genal comb. This is illustrated by Table II, which lists the systematic position of fifteen genera of fleas according to certain authors since 1915, and clearly shows how confused (and confusing) the higher classification of fleas has been. These groups of fleas have been placed in 21 distinct subfamilies, while twelve have been ascribed to at least two separate families during their meanderings in systematics. Thanks largely to Jordan's efforts, the incongruities responsible for the checkered career of these genera were shown to be due to merely superficial resemblances or differences, and today fourteen of the above genera are placed in one family, where they fall into what is now known to consist of three subfamilies. For example, although Rothschild explicitly described *Catallagia* as essentially a *Neopsylla* without a genal comb, the two nevertheless have been placed by other workers in two separate families only because of this difference. *Phalacropsylla* bears a genal ctenidium like *Neopsylla* and is closely related to it and to *Catallagia*, but since it lacks a frontal tubercle, it has been placed in one subfamily, while *Neopsylla* was assigned to another. Jordan pioneered in showing that all three are hystrichopsyllid fleas and are in the same subfamily taxon, although it should be borne in mind that in 1948 he employed family and subfamily endings where he and we now would use subfamilial and tribal designations respectively. Likewise, although *Anomiopsyllus* and *Megarthroglossus* have only one row of bristles on terga II–VII, as do most pulicids, this was rightly regarded by Jordan as being due to reduction or specialisation, and not as being indicative of affinity. Other workers were misled by such characters or by too great reliance on the presence or absence of an interantennal sulcus.

It is relatively easy to criticise a scheme of classification and note errors and inconsistencies, but extremely difficult to propose a superior alternative. Probably Jordan's greatest contribution to the study of Siphonaptera has been the development of a system of classification of the higher categories, thereby ending literal chaos. This significant advance in systematics is based upon his sound background in morphology, coupled with an imaginative insight which enabled him to place new and fertile interpretations upon the relationships of genera, and the ability to consider new approaches as well as established methodology. The Order Siphonaptera seems unique concerning the enormous differences of opinion regarding familial assignment of major genera, as illustrated in Table II. The status of many other genera in the Order has been just as perplexing. The first taxonomic key which even attempted to cope with the many aberrant groups of fleas was that of Jordan in 1948 (21), and this actually is a superb outline of the classification of fleas. Although by definition the key is not wholly inclusive, since the book dealt with arthropods of medical importance, Jordan somehow managed to include in the key the great majority of the subfamilies of fleas. As a result, this chapter has been of incalculable assistance in the identification of fleas from remote areas since many exotic fleas simply would not fit anywhere in previous systems of classification. It cannot be overemphasised that the taxonomic characters used in this key were, to a great extent, wholly original and were not even mentioned by earlier workers, and are examples of Jordan's unusual interpretive powers. Among these original features are all save one of those listed for the superfamilies, and such structures as the vincula of the thorax, apical spines on the metanotom, and a transparent collar over the base of the anal tergum, all of which were formerly completely overlooked or disregarded. The path opened by the pioneer was readily followed by other workers, and Hopkins and Miriam Rothschild (5) based their excellent classification upon that introduced by Jordan in 1948 and upon unpublished notes especially prepared for them at their request. G. P. Holland and F. G. A. M. Smit, workers of the highest standards, and other colleagues have also readily adopted these tenets.

The reader may be surprised that Jordan's epochal classification was not published until some fifty years after he first became interested in Siphonaptera. However, this apparent procrastination to a great extent explains why this scheme of systematics is so superior. Jordan deliberately waited as long as possible so that the maximum number of missing links and intermediate forms would be discovered. In the interim he went over the Tring collection many, many times, noting and studying every possible structure that might indicate relationship rather than similarities. This was enormously difficult, since so many fleas lack close relatives, and since similar morphological traits seem to occur spontaneously in apparently unrelated genera, while seemingly close forms often differ strikingly in a few particulars. Colleagues who visited Tring were astounded at Jordan's tremendous memory for detail, which enabled him to note an obscure characteristic in a species seen for the first time and then unerringly to point out, seemingly without effort, how the same feature occurred sporadically elsewhere in the order. Recitation of detail, however, did not interfere with his making sound generalisations as well. Only when all these pieces eventually began to fit in the puzzle did Jordan decide it was not premature to publish his ideas of classification.

We are also much indebted to Jordan for exquisitely illustrating evolutionary trends within the Order Siphonaptera in 1950 (23) and for simultaneously citing morphological details of use in determining the original affinities of this rather anomalous group of insects. Such an interesting and learned article could be written only by one who knew the comparative morphology of insects in general and was thoroughly familiar with the external anatomy of all types of fleas. Among the thought-provoking philosophical statements is " the anterior end of the body (of an insect) provides for the continuity of life in the individual and the terminal segments take care of the continuity of the species." This article is crammed with expert generalisations posing questions that will stimulate the students of the Order for years. Among these may be mentioned the absence of a true comb on the occiput, the mesonotum, and the sterna of fleas ; as well as the consistent pattern of intercalary bristles on the posterior row on the terga.

Thus far we have been discussing Jordan's contributions in the field of pure systematics, but his researches also have directly assisted the medical scientist. In 1926 (9) he pointed out that the Advisory Commission on Plague forgot to heed its own admonition that " experimenters have in many cases taken no note of, or have not been able to identify, the fleas with which they were concerned. This has given rise to confusion and may no doubt account to some extent for discrepancies in the results obtained ". Instead of acting on its own advice, the Commission assumed that *all* pale fleas were *X. cheopis*, the vector of plague. One reason why the theory of transmission of plague by *X. cheopis* met opposition was that there was no plague in areas such as Madras where "*X. cheopis* " was common. However, as long ago as 1908, Jordan and Rothschild theorised that more than one species of fleas had been present in the experiments undertaken by the Commission. It remained for N. C. Rothschild to demonstrate that there were two other *Xenopsylla* common on rats in India, *X. astia* and *X. brasiliensis*, and Hirst then speculated that the distribution of these fleas might be connected with the distribution of plague. The Tring specialists thereupon showed that the " pale flea " in the non-endemic areas was generally *X. astia*, an inefficient vector of plague. A similar condition occurred when plague authorities in Africa identified the local vector as " *X. astia* ". It seemed strange that *X. astia* could be an inefficient vector in India and a highly efficient one in Africa, but the mystery was solved when Jordan and Rothschild proved that these African " *X. astia* " were in reality *X. nubicus*.

Taxonomic treatises are, by definition, generally of little interest except to specialists in the specific field, and descriptive papers are particularly apt to be read only when under duress. However, Jordan has managed to enliven many of his papers by virtue of a fine sense of humour, which showed to best advantage when he was addressing an audience, as at the international meetings. In 1940, when discussing subspecies (16), Jordan wrote " To go ahunting the flea in the wide and open spaces may sound rather funny, but I can assure you that it requires more time and patience than hunting any of the larger European animals. It may even happen that the object of your search turns on you, which makes it a ticklish affair that leads to bloodshed ". At another time he said " it will interest the fair sex present at this meeting that the male flea has one more ganglion than the female, and that his nervous system is therefore regarded as being of a more primitive type " (23).

A scientist's contributions of course cannot be evaluated or measured merely by the output of articles, regardless of their number or worth. Among the more intangible factors is the rendering of great service as a counsellor, teacher or friend. Jordan's assistance must have materially benefited N. C. Rothschild in the preparation of his many notable papers on Siphonaptera. Many other workers, however, are also much indebted to Jordan for unstinted co-operation and guidance. When I first felt forced to trouble Dr. Jordan with questions the answers to which I could not find in the literature, he not only kindly and immediately answered an unknown novice, but volunteered to verify the status of allegedly new species. He did far more than that, and of his own volition he prepared erudite concise diagnoses to assist me, and made essential comparisons with related forms. He also sent specimens which were not represented in any U.S. collections. This generous assistance soon reached such proportions that Dr. Jordan literally would spend days in the most detailed study of many specimens in order to establish the subspecific status of some exotic flea I sent him. Despite my protests, this splendid scientist insisted on preparing these thorough analyses, attempting to ease my qualms by saying that by doing all this he himself learned more about fleas. Knowing how many more important things he had to do, the only practical course was to refrain from bothering him lest he put aside some personal project and consider only the needs of his colleagues. If Jordan was sent a new flea which was the same as one he was on the verge of describing from material in the Tring collection, he frequently insisted that the other worker describe it, and submitted expert diagnoses to make the task easier.

His personal letters often contain invaluable previews of his concepts of classification, sketches illustrating obscure points, suggestions about taxonomic principles, words of encouragement, and pertinent examples drawn from all phases of natural history. I recall a fine discourse on Lepidoptera in which Jordan mentioned that the butterflies of the southern mountains of Borneo were essentially the same as those on Mt. Kinabalu. In reply I pointed out with regret that the joint U.S. Army-Colonial Office Medical Research Unit laboriously had to go to remote Mt. Trus Madi to establish that the same chiggers and fleas occur there as on Mt. Kinabalu, despite reports in the literature indicating that the Kinabalu fauna was peculiarly indigenous.

One cannot list Jordan's achievements in this field without crediting him with having done a great deal to demonstrate to ornithologists and mammalogists that collecting ectoparasites directly benefits these scientists as well as the entomologist. The remarkable occurrence of South American rodent fleas on seabirds in the Antarctic is a case in point (17, 24).

Fine personal attributes are evident throughout Jordan's articles and have helped him earn universal high regard. As indicated several times above, Jordan has always been extremely loath to criticise any colleague, even though the provocation upon occasion was certainly great. When criticism was invited, it was given with the utmost tact, and hence with maximum effect. He invariably readily and carefully acknowledged his colleagues whenever the opportunity arose, just as he was the first to call attention to his own errors.

The point has already been made that Jordan's taxonomic work has consistently been extremely accurate. It remains to be emphasised that the papers written in the last ten years, when he was in his eighties and nineties, are the finest he has ever done as regards concepts of classification and relationships of fleas. In fact, the only truly satisfactory classification of fleas was published during this period, and the descriptive papers are still models. Further, his drawings are still excellent, even though Dr. Jordan expresses the fear that his hand is no longer as steady as it once was. This ability to continue first-class professional research at such an advanced age, and to work late hours night after night, is indeed more than a marvel. It is an inspiration to the rest of us and a promise of what the new science of geriatrics may someday bring to all.

Remarkable as Dr. Jordan is, the log of his attainments is testimony to more than to his wonderful temperament and talents. It is also an expression of the loving care and assistance of his devoted daughters, Ada and Hilda Jordan, of the friendship and collaborative efforts of Lord Walter Rothschild and the Hon. N. C. Rothschild and other colleagues at Tring, and of the academic freedom and wholesome scientific atmosphere of the country that became his home.

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KARL JORDAN'S CONTRIBUTION TO OUR KNOWLEDGE OF FLEAS ASSOCIATED WITH DISEASE.

By P. A. Buxton.

A worker in medical entomology may present his contribution. To him the names of Karl Jordan, linked with that of N. C. Rothschild, are those of the men who reduced the Siphonaptera, the fleas, to systematic order.

Medical entomologists are frequently occupied in a specialised form of natural history. For instance, the student of plague finds himself in a fascinating, exceedingly complex, world : for the simple statement that the plague bacillus is conveyed from rat to man by fleas is only a fraction of the truth. The fleas, for instance, may belong to a variety of different species. Some are able to flourish in a restricted area or only in the conditions prevalent inside the rat's nest. Others may breed successfully in warehouses or ships ; not being narrowly limited by climatic factors these fleas may become almost cosmopolitan. Some fleas again will feed only on one sort of rat, others on many animals, including numerous rodents and perhaps man. The last point, which would perhaps be trivial if we could view the whole world of nature, is vital to the human race, because plague in our species depends upon these insects biting both rats and man.

Plague, even more than other epidemics, appears erratic and unpredictable : it has always seemed in a real sense an "act of God". Though much still remains unexplained, we have known for half a century that much of the epidemiology may be explained by what we know about the natural history of the "tropical rat flea", *Xenopsylla cheopis*. This insect can live under a wide variety of conditions ; it can inhabit grain stores and houses ; it feeds on many sorts of rats in the field, in the house or in the ship ; it bites man readily. Because of these characteristics it is the most effective transmitter of the plague bacillus from rat to man.

If we look back into the history of this insect, *X. cheopis*, we find that the first specimens were collected by N. C. Rothschild. He was not investigating plague but was studying fleas for their own sake, just as some other naturalist might have studied mosses or butterflies. He found these fleas in the valley of the Nile, living for the most part on wild rodents such as gerbills and jerboas. That work was published in 1903. A few years later (1908) the subject had advanced to the point where Rothschild and Jordan could publish their review of the non-combed eyed Siphonaptera. They knew that *X. cheopis* was widely distributed about the world, often on domestic rats, and they presumed that it was the transmitter of bubonic plague. They had already discovered that there were a number of closely related species of fleas, and they dealt with the systematic questions so far as possible, laying the foundation of entomological work on the disease. Failure to make use of entomology led to much confusion among those who studied plague in India. When the entomogical basis of the matter was recognised, many confusing and contradictory points became clear. It was found, for instance, that the absence of plague from some areas was to be associated with the fact that the rat fleas there were not *Xenopsylla cheopis* but *astia*. The contribution that Jordan and Rothschild have made is that they have shown, once and for all, how specimens of fleas should be studied, described and catalogued. They have added immensely to the number of species known, and produced a system for precise scholarly identification.

KARL JORDAN'S CONTRIBUTION TO CURRENT CONCEPTS IN SYSTEMATICS AND EVOLUTION.

By Ernst Mayr.

It is a particular pleasure to be able to contribute an essay to this volume which honours one of the great biological thinkers of our time. I have admired Karl Jordan and his work since my student days and I am most grateful to the editors of this volume for this opportunity to express my admiration. It would seem particularly fitting that a non-entomologist should discuss Jordan's contributions to systematics and to the study of evolution, since Jordan has been at all times, first and foremost a biologist, even though working with insects as study material.

There is no need for me to stress Jordan's contributions to the field of entomology. They are universally appreciated and his election as Honorary Life President of the International Congresses of Entomology is one of many visible tokens of his prestige in the entomological world. What is not known among entomologists, however, and even less among most general biologists, is the fact that Jordan has made a number of highly important conceptual contributions in the fields of systematics and evolution. Yet his name is rarely mentioned in histories of the development of these fields. Possible reasons for this neglect are manifold, but it is evident that the basic one is that Jordan was far ahead of his time and thus was destined to suffer the fate of so many pioneers. A second reason is that he worked with a material (natural populations) and with methods (non-experimental) that were unpopular among the laboratory biologists of his time. He has always been averse to the spectacular which, as the history of biology shows, very often monopolises attention, no matter how soon afterwards it is shown to be wrong. It is a curious paradox that the name of the investigator who finds the right answers is likely to be forgotten, because his findings are incorporated anonymously into the treasury of common knowledge and accepted theory. That this has been Jordan's fate to a considerable extent, will be revealed in the subsequent analysis.

It has been pointed out recently that most "histories" of evolution are actually "pre-histories". Their detailed treatment stops around 1860, precisely at the time when the development of the modern concepts began subsequent to the publication of Darwin's *Origin of Species* in 1859. The reluctance of historians to deal with the modern developments is understandable, since only a specialist can truly evaluate the significance of various contributions. With respect to systematic and evolutionary concepts there is the additional difficulty that much of the documentation is hidden away in taxonomic monographs or in rather specialised writings of naturalists. Furthermore, each author stands on the shoulders of his predecessors and with certain concepts it is hard to decide who deserves the greater credit: he who first vaguely mentioned a new idea, he who first clearly formulated it, or he who supplied final proof. Also there has been much parallelism, so that many conceptual advances have been made by several authors independently. In view of this it would be unwise to assert too dogmatically which particular concept was pioneered by Jordan. To determine this unequivocally would require an analysis of the writings of all of Jordan's contemporaries and predecessors similar to this one. The time has not yet come for such an analysis and this evaluation of Jordan's contribution is limited to the available evidence. It may have to be modified after the detailed history of various branches of natural history has been written.

Jordan is still working actively and has published only recently highly competent papers in the special fields in which he is an acknowledged master. Those publications, however, in which he made his most important conceptual contributions were published principally during the period from 1895 to 1911. In addition to a number of shorter papers (which are quoted in the bibliography), they include several major treatises which have since become classics. Among these are two general papers (on mechanical selection, 1896, and on geographical versus nongeographical variation, 1905) and a number of entomological monographs, prepared in joint authorship with Lord Rothschild, in which most of the general discussions were written and are usually signed by K. Jordan (eastern Papilios 1895, Sphingidae 1903, and American Papilios 1906).

The turn of the century was intellectually an exciting period in the history of systematics and evolution. The theory of evolution had by then been almost universally accepted by biologists, yet they were still groping for the correct interpretation of the causes of evolution. As far as the " material of evolution " is concerned the year 1900, as the birthdate of the science of genetics, must be considered the starting point of our knowledge. The battles about the mode of speciation, the existence of natural selection, and the meaning of mimicry and of polymorphism were at their height. Jordan entered all these battles with enthusiasm and conviction, and one is filled with admiration bordering on awe when one compares Jordan's discussions with those of most of his contemporaries. In almost every case it is Jordan who is right, and his formulations and solutions of biological problems are very often superior to those offered by other biologists during the succeeding fifty years.

Jordan's Biological Philosophy

Jordan has had the happy faculty of synthesising new concepts of biology by fusing the best elements of various schools of thought. Through his education at the University of Göttingen, he received a training in the best tradition of German zoology. Among his teachers was Ehlers, a competent comparative anatomist of invertebrates, who brought him in contact with the battles then raging between Weismann, Haacke, Eimer, Haeckel, and others, concerning the causes of evolutionary change. Through his entomological interests Jordan came in contact with an experienced group of insect collectors and breeders. Equally, if not more important, after his transfer to Tring, was his steady contact with Rothschild and with Hartert. Rothschild's great enthusiasm, particularly for the study of island faunas, was infectious, and Hartert at that period had become the leader of that group of ornithologists who were fighting for the consistent application of trinomials, for the downgrading of isolated allopatric populations from the rank of species to that of subspecies (wherever possible), and for a broadening of the species concept (Stresemann 1951.) Hartert (1859–1934), a great naturalist and practical systematist, never wrote a major paper on principles of evolution or on the new sytematics, but there is no denying his influence on Jordan, particularly during the formative years 1893–1895. Yet, a careful study of the publications of the Tring triumvirate (Rothschild, Hartert, Jordan) shows quite clearly that Jordan, perhaps as a consequence of his more complete university training and his greater interest in general biology, soon surpassed his teachers, when it came to developing new concepts in systematics and evolution.

Jordan's entire work in the fields of entomology, systematics, and evolution is founded on a few basic beliefs. They relate to the position of systematics in biology, the application of the concept of evolution to taxonomy, the meaning of variability, and the working methods of the scientist :

Systematics and biology.—There have always been two kinds of taxonomists : those for whom species of animals and plants are like postage stamps to be collected or described merely for the sake of rarity or novelty, and those others for whom systematics is an important branch of biology. Jordan has always included himself enthusiastically in the latter camp. He expressed repeatedly (e.g. 1905 : 150) his regret over the short-sightedness of so many laboratory biologists who thought that nothing could be learned from systematics because they themselves knew nothing about this field and had contact only with the stamp collecting type of taxonomists. " Classification, as we know, has the reputation of being as dry as our cabinet specimens—if not mouldy—and of having an interest only for those who work at the special group of animals classified. There are even biologists of fame who, in their misguided wisdom, scoff at systematics and look down upon this kind of work as more or less fruitless . . . I take the opportunity . . . of stating emphatically that sound systematics are the only safe basis upon which can be built up sound theories as to the evolution of the diversified world of live beings " (1911 : 385.).

It cannot be denied, admitted Jordan, that systematics is unthinkable without painstaking attention to a great deal of detail. Without this there is the danger of committing glaring errors such as Darwin's statement that the birds of Madeira and the Canary Islands have not been modified in comparison to European birds. The subsequent careful studies of Hartert and other bird taxonomists have proved the error of this statement. " A precise knowledge of the lowest systematic units which only the systematist can produce is not only the foundation for a valid theory of evolution but also a necessity for the correct placing of the many units into a system " (1905 : 153). It was the lesson which Jordan had learned as a zoology student at the university, that the taxonomist has a great deal of information of vital significance to the general biologist, which Jordan stressed throughout his career. For long it seemed like a hopeless endeavour to bring this point home, but the increasingly closer collaboration between taxonomists and experimental biologists during the past two decades proves that the point has finally been made. Jordan has contributed his share toward the victory of the idea that every taxonomist must have a broad training in general biology, and that every biologist must know and understand the important generalisations that come from the field of systematics.

Taxonomy and evolution.—Jordan has been an enthusiastic evolutionist from the beginning of his career. One might go so far as to say that all his research is ultimately directed toward adding further light on the processes of evolution.

The ambiguous rôle of the theory of evolution in the development of the theories of systematics is often commented on. Prior to Darwin the system of animals was merely a system of similarities. But ever since 1859 there has been an argument, which has not yet been unequivocally decided, whether the system should only serve the purely practical aims of the proper cataloguing and pigeon-holing of specimens or whether, as a consequence of the theory of evolution, animals should be classified on the basis of presumed relationships. Jordan is quite emphatically of the second opinion. He cites (1905) one case after the other where a modification of the classification on the basis of presumed relationships has lead to a considerable improvement of the distributional picture and to a better understanding of biological phenomena. For instance, if the West African butterfly *Papilio zalmoxis* is removed from the large Oriental *Aristolochia* feeders where this species was placed by all specialists on account of a superficial resemblance, and associated with various small African species with which it is really related, the remarkable fact is at once apparent that in spite of the presence of food plants there are no *Aristolochia* feeders in Africa. Jordan cites numerous cases from the writings of Wallace, Scharff, Eimer, and others where complex zoogeographic situations are at once clarified as soon as the respective species are classified not on the basis of superficial resemblance, but on that of relationship as revealed by totality of characters including internal ones. " The aim of the systematist as such is the establishment, on reasoned evidence, of the degree of relationship between the forms with which he is concerned, the evidence being furnished by the specimens and the bionomics of the species and varieties to which the specimens belong " (1911 : 386).

The meaning of variability.—One of the most revolutionary changes of concept in biology has been the replacement of typological thinking by thinking in terms of populations. According to this concept no two individuals or biological events are exactly the same and processes in biology can be understood only by a study of variation. The greatest of Jordan's papers (1905) was devoted to a discussion of the meaning of variation and the light it sheds on an understanding of evolutionary phenomena. The study of variation is an absolute necessity in the work of the taxonomist. Jordan, partly influenced by Rothschild and Hartert, came to understand very early how important it was to study adequate samples of as many natural populations as possible " . . . Nowadays systematics comprehend more and more that a few specimens of each species are insufficient for a serious study, and hence try to bring together long series from every locality " (1896 : 447) (*see* also 1905 : 182).

Methods of the scientist.—Jordan, who himself has had such a broad background, has always emphasised a broad approach and a balanced analysis. He himself, superb master though he has become of certain groups of insects, has always tried to remain broad in his interests. In the field of entomology he was equally at home among beetles, butterflies, moths and siphonaptera. When analysing a given taxonomic situation he has stressed the importance of utilising the greatest number of characters, as we shall discuss below. He believes that by analogy the same working principle should be applied to the study of evolution. He warned the evolutionist not to be deceived by an artificial system of factors just as the taxonomist must beware of an artificial system of characters. " Scientific systematics utilises so far as possible all the attributes of the forms that are to be classified in order to determine their real relationship.

If there is a contradiction between one organ and another, there is either an error in observation or in interpretation. The research on one organ serves as a control for the research on the other, and this permits the recognition and elimination of errors. The same method must be used in the investigation of the causes of evolution if one does not want to be satisfied with an artificial explanation of the origin of the gaps between species which corresponds to an artificial system of classification " (1905 : 210). The common sense and the mature balance of mind which is expressed in this quotation has always been characteristic of Jordan. It has been characteristic of his taxonomic decisions and of his philosophy of nomenclature. It is not my task here to discuss Jordan's contribution toward the theory of nomenclature, and more specifically toward the stabilisation of nomenclature which he so ardently desires, but mention of his attitude toward nomenclature must be made in this context. " The philosophic aspect of systematics is unfortunately much obscured . . . due in a large measure to an unduly great importance being attributed to the mere giving of names. Nomenclature is the servant of science, but has in many houses the position of master " (1911 : 386).

CONTRIBUTIONS TO CONCEPTS OF SYSTEMATICS.

It has become fashionable to apply the label " new systematics " to the set of concepts that is now prevailing in the field of taxonomy. The silent assumption is made that these concepts are new. Actually their roots go back to the middle of the nineteenth century or earlier and it would be difficult to name a single concept that was not formulated at least thirty or forty years ago. What may come as a revelation to some of the younger students in this field is the discovery of the extent to which this " modern " philosophy is present in all of its completeness in the classical publications of Jordan. While much of it had been expressed casually or timidly by earlier authors, it is in the writings of Jordan that we find many of these concepts for the first-time stated fully and in detail. His broad knowledge of the contemporary zoological literature and his contacts with students of other kinds of animals as well as with general biologists, permitted him to develop many concepts in advance of his contemporaries. If any one deserves to be called the father of the new systematics it is Jordan. His influence on entomologists and taxonomists in general cannot be exaggerated. More specifically this influence is apparent in the development of thorough taxonomic techniques, a new evaluation of the infra-specific categories and his contribution toward the development of the modern species concept.

Taxonomic techniques.—We have mentioned above that Jordan has repeatedly stressed the need for the study of large series of specimens and for the utilisation of as many additional taxonomic characters, both external and internal ones, as can possibly be found. In his studies of butterflies he emphasised the taxonomic importance of such structural characters as scales and wing venation, and his extensive studies of the individual and geographic variation of the sexual armatures of both male and female butterflies (1896, 1905) have been hardly surpassed since. He is undoubtedly the pioneer in studying the variability of these structures in a large number of specimens from a single population and in following up their geographical variation. But he was not satisfied to use this evidence for purely taxonomic purposes, but utilised it, as we shall presently see, as an elegant proof of geographic speciation.

His concepts of the validity of taxonomic characters were far ahead of his time and many contemporary taxonomists might learn from what Jordan said in 1905 (p. 171). " One speaks in phylogeny often of generic characters as opposed to specific ones. There is, however, no valid definition of generic morphological characters as there is none of specific ones. To call the above described variability a change in generic characters because the diagnosis of genera in our somewhat superficial taxonomy of butterflies is frequently based only on differences in wing venation, would be circular reasoning. Differences in wing venation may be either individual, specific, generic, or even a taxonomic criterion for subfamilies and higher systematic categories ". He is convinced that one cannot hope to understand the variation of taxonomic characters by studying individuals. In order to understand the variability of species, it is necessary, he says, to study the offspring of a single female or " the individuals flying [he speaks of butterflies] in the same locality," in other words local populations (1896 : 430).

The subspecies.—In the field of systematics the name Tring or Tring School is associated with definite concepts such as a liberal use of subspecies and an attempt to arrange natural populations into polytypic species. There is little doubt that Hartert was the original leader of this team since he had fought for these concepts in print as early as 1891 (before coming to Tring). Little of this philosophy was noticeable in Jordan's early papers on beetles; for instance, among several hundred descriptions of new beetles published in 1894, there are only a few subspecies. But as soon as he started working on the species of *Papilio* with their immense geographic variation, he applied wholeheartedly the new subspecific concept as explained in his introduction (pp. 168–182) of Rothschild's revision of the Papilios of the eastern hemisphere (1895). Up to that time there had been great confusion as to the correct usage of the terms subspecies, variety and aberration. When the Tring triumvirate started publishing the *Novitates Zoologicae* they found it necessary to clear up this confusion in the following editorial preamble (1894, *Novit. Zool.* **1** : 1) :—

" The term ' variety,' especially among entomologists, has been indiscriminately used to denote an individual variation within a species as well as climatic or geographical races. We therefore, to avoid all possible errors, have determined to discard the term ' variety ' altogether. To denote individual variations we shall in this periodical, employ the word aberration, and for geographical forms, which cannot rank as full species, the term subspecies.

Editors."

At this period the introduction of subspecies into taxonomy was vigorously opposed by the older generation. The subspecies was still a relatively new concept and no unanimity was yet achieved as to its definition or application. Jordan took a stand on both these points. " A subspecies is a localised group of individuals of a species, the mean of the characters of which is different from the mean of the characters of all the other localised groups, and which will, under favourable circumstances, fuse together with other groups " (1896 : 447). He realises that this definition fails to make a clear distinction between populations that are sufficiently distinct to deserve to be named as subspecies and other populations that are not. “ The above definition has not had regard to the degree of divergence attained by the localised form. Now, we ask, which then is the lower limit of application of the term ‘subspecies’?” On the basis of cases where one sex is clearly different in two places while the other one is identical, “ we shall have to use the term ‘ subspecies ’ when a localised variation is such that about half of the individuals belong to the varietal form. All lower degrees of localised variation may be termed ‘ localised aberration ’ ” (1896 : 447–448). It is evident that at this date there was still some difficulty in distinguishing between individual and geographic variation as well as in specifying the degree of the distinctness of that half of the form which is different. In subsequent years Jordan has been particularly interested in the biological problem of the meeting of two subspecies with special emphasis on a most intriguing and puzzling case among fleas which he had discovered (1938, 1940). As far as isolated subspecies are concerned, he adopted Hartert’s viewpoint . . . “ that geographical separation of different forms cannot be an *a priori* criterion of specific distinctness, though this has often enough been alleged” (1896 : 431).

The species concept.—Again and again in his writings Jordan comes to grips with the species concept. He realises clearly that this concept is not only fundamental for the practical work of systematics, but equally crucial for studies of speciation and evolution, as is so painfully evident from the writings of those who have ignored the species problem in their discussions. In order to understand and evaluate Jordan’s own viewpoint and his contributions to the subject, it will be necessary to outline the current status of this problem. It is rather evident from the fact that the controversy is still continuing (Gregg, 1950; Burma, 1954; Burma and Mayr, 1949) that a full understanding of the species problem has not yet been reached. After a thorough study of most of the literature on this subject, I have come to the startling conclusion that the disagreement is due to the fact that there is in existence not merely one but actually three entirely different species concepts. All past arguments and discussions have suffered from the fact that an author has either championed one of the three concepts against the others or has wavered between two of these without realising it.

The first of these concepts is the typological one which goes back to the Eidos (εἴδοζ) of Plato. Such a species is a “ different thing ”. Implicit in this concept is that variation as such is unimportant since it represents only the “ shadows ” of the Eidos. Translated into biology the typological concept becomes the morphological species concept. Certain individuals are a different species “ because they are different ”. When a minerologist speaks of “ species of minerals ” or a physicist of “ nuclear species ” he has this typological species concept in mind. This concept is still widespread in certain branches of invertebrate zoology and in paleontology. The objections against this concept are manifold and have been stated by Jordan with great clarity and vigour. First of all it is a strictly subjective concept. “ It would almost appear, in fact, as if a ‘ species ’ is that which a respective author chooses to consider a ‘ species ’ ” (1896 : 426). Inevitably this concept cannot be applied without all sorts of inconsistencies. “ If it is the presence of morphological difference which leads us to split up into the one case, and the absence of such difference in the other case to unite, why then are *Distomum*, *Redia*, and *Cercaria* ; *Rhabdomena* and *Rhabditis* ; *Vanessa levana* and its offspring *prorsa*, the same species?

Morphological difference alone is not a criterion of specific distinctness " (1896 : 434). After citing numerous other cases which show the worthlessness of a typological-morphological species concept, he comes " to the conclusion that morphological differences of any kind and degree are not decisive criteria as to specific distinctness ; the systematist actually sinks his species in spite of distinguishing characters as soon as it is proved that the morphologically different forms appear among the offspring of the same female. The most general case of bodily difference which is not regarded as being specific is the difference between males and females ; notwithstanding the great dissimilarity which the sexes so often exhibit, not only in the reproductive organs, but also in other morphological characters, the systematist puts male and female together in one species, and hence makes at once the concession that his term ' species ' is not a purely morphological one, but that the higher criterion of the term is of a physiological kind " (1896 : 436). One has only to read the papers of De Vries and other contemporary plant breeders and early Mendelians to appreciate how far ahead of them Jordan was in his thinking. Having laid to rest the morphological concept so decisively, Jordan was ready to investigate what the physiological criteria are that characterise species. This led him to a consideration of the second species concept.

This is altogether different from the typological species. It does not deal with things, describing their degree of difference, but specifies a relationship. It is a concept like the word " brother " which has a meaning only with reference to some other object. This " biological " or " non-dimensional " species concept describes the relationship of two natural populations that co-exist at the same locality and specifies this relationship as " non-interbreeding ". The concept has been designated as " objective " because it can be defined as objectively as the word "brother" or as many similar designations of relationship. It has nothing to do with the objectivity of the concept itself that its *application* to taxonomic situations may occasionally run into difficulties just as it is occasionally difficult to establish the father of a baby even though there is nothing subjective about the biological concept "father" itself.

The revolt against the typological species concept and the attempt to replace it by a more biological concept had started long before Jordan. Indeed it is this concept of the non-dimensional species, expressing the relationship of non-interbreeding among sympatric populations of a single locality, which was the foundation of the original biological species concept of John Ray (1692), of that of Linnaeus, and of that of all local naturalists since. Although they had arrived at this concept empirically they had not thought it through sufficiently to describe it and define it unequivocally. That a species is a reproductively isolated population had also been previously expressed. Eimer, for instance, had spoken of species as " groups of individuals modified in such a manner that interbreeding between them and other groups no longer takes place or is not possible with success indefinitely " (1889 : 16). Poulton (1903 : 94) had said that " the idea of a species as an interbreeding community, as symgamic, is I believe the more or less acknowledged foundation of the importance given to transition " in geographic variation. Yet in all my search through the literature I have not found a single statement by any other author which indicates an understanding equal to that of Jordan. He was the first to point out the completely objective nature of the species concept as a measure of relationship in a non-dimensional situation (1905 : 157) : " . . . Individuals connected by blood relationship form a single faunistic unit in an area, to which unit we must add all the other individuals of the area which resemble them. This is the cornerstone of the building of the systematist and the starting point for an exact analysis of the correctness of the theory of evolution." And speaking of the single locality of the neighbourhood of Goettingen, his alma mater, he continues : " The three common *Pieris* of the gardens of Goettingen, the carab beetles of the Hainberg, the physopodes in the flowers of the Botanical Garden, the mice on the fields of the Weend, the bembids on the sand of the shore of the Leine, they all prove that the living inhabitants of a region are not a chaotic mass of intergrading groups of individuals, but that they are composed of a finite number of distinct units which are sharply delimited against each other and each of which forms a closed unit . . . The units, of which the fauna of an area is composed, are separated from each other by gaps which at this point are not bridged by anything. This is a fact which can be tested by any observer. Indeed all faunistic activity begins with the searching out of these units. A list of the species that occur in a region is an enumeration of such independent units which with Linneaus we call species " (1905 : 157). This masterful statement, published in 1905, is as true today as it was then. If it had not been ignored by so many taxonomists and non-taxonomists since that time, we could have saved ourselves much useless argument.

The third species concept is that of the multi-dimensional species. While the non-dimensional species defines a relationship of two populations, the multi-dimensional species is a grouping of populations. It is thus essentially the same as any higher category, a grouping of units of the next lower category, as the genus is for instance, a grouping of species. This third species concept then is a collective concept and, as all collective concepts, it lacks in principle the precision and objectivity which is generally inherent in relational concepts. If we group a number of geographically representative populations under the heading of a single polytypic species it is inevitable that we have to make a number of subjective judgements. As long as these populations are interbreeding and intergrading with each other there is usually little conceptual difficulty. In such cases it is generally granted that the combined populations conform to the criterion of the non-dimensional species concept and form a single reproductive community. As soon as populations are added to this polytypic species that are separated in space or time the judgement becomes truly subjective. The classifying taxonomist is faced here with the same situation as he is on the generic level when he must make a decision on the status of an aberrant species which is considered congeneric by some authors and generically different by others.

It was an inevitable consequence of the great period of geographical exploration that the non-dimensional species of the local naturalist had to be expanded into a multi-dimensional species, a geographically variable species. Early authors were confused as to what to do with geographical varieties nomenclaturally. Some, like Pallas, described the differing populations of new localities as " varieties," and so did Linnaeus himself in some cases. Other authors, limiting themselves rigidly to the classical binominal system of Linnaeus, called each of these different populations a separate species. Eventually a system of triple names won out, with the geographical varieties listed as subspecies.

That this new method produced a basic conflict of two very different species concepts was overlooked either consciously or unconsciously. The first author, I believe, who clearly realised that the non-dimensional species of Linnaeus and the multi-dimensional species that was so rapidly gaining favour in the second half of the nineteenth century, are not one and the same thing was O. Kleinschmidt. He restricted the term species to the non-dimensional relation and coined for the collective species the term " Formenkreis," later emended by Rensch into " Rassenkreis." This action, though inconvenient for practical purposes, was entirely logical. It also presented the historical developments correctly. The recent attempt to restrict the term species to the multi-dimensional concept and to apply the group symbol of symbolic logic to the concept species, as was done by Gregg (1950), is based on a misunderstanding of the historical developments.

It is only natural that Jordan, as a member of the Tring team, endorsed wholeheartedly the application of the concept of polytypic species to natural populations. Hartert already earlier had come to the conclusion that isolated populations should not be excluded from polytypic species if they seemed to belong to them on the basis of corroborating evidence. Jordan repeatedly explained why such a decision is inevitable. Since it is known from experiments and observation that strikingly different individuals may be members of a single interbreeding population " it is *a priori* evident that also geographically separated forms, in spite of their being morphologically distinct and in spite of their not being connected with one another by intergradations, can very well be subspecies of one species, i.e. that they can under favourable circumstances fuse into one form. The actual proof of specific distinctness the systematist as such cannot bring . . . we work with the mental reservation that the specific distinctness of our species novae deduced from morphological differences will be corroborated by biology . . . " (1896 ; 450–451). The viewpoint of the Tring school was at first not well received among taxonomists, and Jordan found it necessary to return to this argument in 1905. He uses a discussion of the geographic variation in the genitalic structures and other taxonomic characters of the butterfly *Papilio dardanus* to prove in a brilliant, closely reasoned argumentation that complete continuity of populations is not necessary in order to permit combining geographically isolated subspecies into polytypic species (1905 : 196–197). The tremendous simplification of classification which these arguments have made possible is now a matter of history. Yet there are some contemporary biologists who still fail to make a distinction between the *reproductive* isolation of sympatric populations, which proves that they are different species, and the *geographic* isolation of allopatric populations, which does not necessarily prove it. I recommend to them reading Jordan's arguments which have as much weight to-day as they had when he first stated them.

In retrospect we begin to understand why taxonomists have had so much difficulty during the past 100 years to apply the species concept to the purely practical task of classifying natural populations. They did not realise that there is no such thing as " the species concept " but rather three different concepts, each of which may permit a different conclusion in a particular situation. Jordan himself was no exception in this respect. In his various attempts at a species definition he wavered between the three stated concepts and finally attempted to include in his species definition criteria taken from all three.

It is still of interest to study his discussion of the species definition as given in 1896 (p. 438). His definition then reads " a species is a group of individuals which is differentiated from all other contemporary groups by one or more characters, and of which the descendants which are fully qualified for propagation form again under all conditions of life one or more groups of individuals differentiated from the descendants of all other groups by one or more characters." It is evident that as a taxonomist he feels that in his practical work he cannot do with a species definition that omits reference to morphological criteria. "The question of specific distinctness or non-distinctness is therefore two-fold: first, one of morphological, and second, one of physiological difference " (1896 : 442). He continues by pointing out that in most cases the systematist is not able to test by experiments the presence of physiological distinction and that therefore he can never prove with certainty from specimens alone whether the distinguishing morphological characters are of specific value or not. However, experience shows that physiological isolation and degree of morphological difference are so closely correlated that one is permitted, in the case of isolated populations, to determine their taxonomic status by comparing their morphological distinctness with that between related species and subspecies. Therefore, " If in a given case we have to decide whether A and B, which live together, are two different species, or two forms of one species, the morphological characters of A compared with those of B and the geographical representatives of B will have to guide us in our judgement " (1896 : 453). " The same kind of evidence we may employ when we have to come to a decision as to the specific distinctness of geographically separated forms which are not connected by intergradation. We must accept as a general law that forms which are connected by all intergradations, or forms which overlap in characters, are specifically identical ; . . ." This statement, made in 1896, (p. 454) is still somewhat vague. By 1905 Jordan had considerably clarified his ideas. He states (1905 : 157) that the working taxonomist is usually faced with two potential difficulties. The first is to decide whether a group of variable specimens from one locality belongs to one species or to several, and the other one whether somewhat different samples from two different localities belong to one or to two species. How can we tell, he asks, whether a certain number of specimens collected at one locality belong to one species or to several. Unfortunately, he answers this question, it is quite impossible to give a general answer. Species criteria must be determined anew for each group of organisms. In some cases only the breeding in the laboratory can supply the final proof, yet, much as the specific criteria change from group to group, there is no evidence that the species concept as such varies from one taxonomic group to another. The study of living populations and the breeding in captivity indicate that the morphological species criteria are correlated with a physiological condition. " We find that the morphological gap between individuals of two different species is accompanied by a physiological difference which is missing in the case of the morphological gap between individuals of one and the same species. This physiological difference has two consequences, namely :

" First, that individuals of a species, no matter how different from each other morphologically, will produce only individuals of their own species and,

" Second, that different species can co-exist in the same area without fusing into a single species " (1905 : 159).

He then continues to summarise his viewpoint in one of the most important passages in the history of biology. " The criterion of the concept species is thus a triple one and each of its three aspects can be investigated : A species has certain morphological characters, does not produce individuals belonging to a different species, and does not fuse with other species. As in 1896 I place great emphasis on this latter point. The non-fusion is the explanation for the immense number of existing species. Nothing keeps the species of an area separated but their own organisation. Individuals of one species live side by side with those of other species so genetically independent as if there had never been any genetic connection between them, as if each species has been created separately. The discovery of this fact led, during Linnaeus' time, to the dogma of the constancy of species. The experience which the observer of the individuals of his district and of his time made was erroneously extended to the individuals of all times and all districts." Here again Jordan emphasises the validity of the species concept for the non-dimensional system. He continues " If non-fusion is the principal criterion of specific difference it follows that one can prove specific distinctness only for those related forms which co-exist in the same area. The work of the systematist must begin with these and when dealing with all presumptive species from different regions he must ask himself whether the differences between them justify the conclusion that these forms could co-exist in the same area " (1905 : 159–160).

There is one among the conventional species criteria in insects to which Jordan paid special attention, difference in the structure of the genitalic armatures. Dufour had asserted that the male genital armatures were different in every species and had proposed the hypothesis that this difference serves as a mechanism to prevent hybridisation between different species and thus preserves the purity of each species. During the fifty years preceding Jordan's paper (1896) on mechanical selection, the idea had become quite universal among entomologists that each species could be diagnosed on the basis of its genitalia and that there was no individual variability with respect to this character. Only few authors such as Kolbe (1887), Perez (1894), and Edwards (1894) had disagreed with this hypothesis. Jordan, however, had *a priori* doubt against this concept " because if the concept of evolution is correct then species differences in the genital organs must have evolved, and the beginning of such differences must be visible already within the species " (1905 : 164). It is the main object of his important 1896 paper to demonstrate individual and geographical variation in these structures. An analysis of twenty-seven species of *Papilio* proved conclusively the existence of geographic variation. Jordan illustrates this on four plates with 189 figures. Each of the examined species of *Papilio* had a diagnostic difference in the structure of the genitalia from every other species of the genus. In 1896 Jordan was therefore convinced that Dufour was at least in part right. However, further studies convinced him that species specific difference in genital morphology is not a necessity. For instance, among 698 studied species of hawk moths (Sphingidae) there were forty-eight which did not differ in their genitalic structures ; at least Jordan was not able to establish differences on the basis of the available material (1905). Jordan thus was the first to prove conclusively that reproductive isolation between species of insects was not necessarily supported by mechanical isolating mechanisms and that the genitalic structures are subject to the same laws of variability as all other taxonomic characters. The aspect of this investigation most pleasing to a modern worker is the method of approach. Jordan did not single out one convenient example to demonstrate his case ; no, he made a complete statistical analysis of all the available species of a whole family. Jordan's work on the variation of genitalic structures in insects is outstanding in its formulation of the problem, procedure and conclusions.

We shall now leave our discussion of Jordan's contributions to the development of the modern species concept and to other phases of the new systematics. Although he left his successors the opportunity to straighten out a few details, such as the relation between non-dimensional and multi-dimensional species concepts, it is evident that he had already developed in broad outlines all the modern views. After Jordan's discussion of the species concept in 1905 substantially no progress was made in the literature of the succeeding thirty years. In fact, in the entire genetic literature I have not found a single discussion of the non-dimensional species which is as penetrating as that of Jordan.

Concepts of Evolution.

Jordan at all times has been of the firm conviction that the taxonomist can make an important contribution to the understanding of the processes of evolution, indeed that no full understanding of evolution is possible without taking into account the conclusions of the taxonomist. For instance, " my object is to demonstrate that there is more in classification than lies at the surface by proving that there exists a very intimate connection between, on the one hand the vexed question of specific distinctness, and on the other hand the elucidation of the factors of evolution to which is due the great diversity of the animal world " (1911 : 386). And among all the evolutionary problems he realised that the systematist was best equipped to solve that of the origin of gaps between species. Such an investigation, he says (1905 : 160), has two aims. First to explore the steps which lead to these gaps, and second to find out what causes are responsible. As far as the method of investigation is concerned he believes that the systematist must find out whether the differences which exist among species are something quite unique or whether they are merely a more advanced stage of the kind of differences which one may find among individuals within a species. His aim then was to solve the problem of speciation by means of the inductive method.

Modes of speciation.—The particular problem as to how one species breaks into several has been the source of bitter argument ever since the theory of evolution was proclaimed. At the time of Jordan's major papers a bitter battle was waging over the right theory of speciation. The general biologists, the geneticists, animal and plant breeders and a minority of the taxonomists were in one camp and the other taxonomists in the other. The argument, in short, was whether or not speciation was possible without geographical segregation. Both Karl Jordan (1905 : 162) and D. S. Jordan at about the same time stated that the theory of sympatric speciation was virtually universally accepted among the biologists of that period. According to this theory individual variants can develop into full species without geographical isolation. It is a historical fact that Bateson, De Vries, and their powerful schools of contemporary geneticists endorsed and postulated this mode of speciation. In the discussion of this problem Jordan notes that at first sight the concept of sympatric speciation appears to be abundantly supported by various facts. One of them is that there are many places on the earth where a great number of closely related species co-exist, as the lemurs on Madagascar, certain groups of insects in the Hawaiian Islands, the marsupials in Australia, and the humming birds in America. However, says Jordan, some authors dissent and have come to the conclusion that one species can split into several only by way of a geographic variety. This concept was first clearly expressed by Moritz Wagner and had since been adopted by a considerable number of taxonomists. " My own investigations completely confirm this theory as I want to demonstrate in the subsequent discussion of the great difference between geographic and non-geographic variation " (1905 : 163).

The theory of evolution postulates that species evolve from incipient species. Darwin and his successors, following up this thought, came to the conclusion that varieties within species are these incipient species. No agreement, however, was reached on the question whether or not all of the many kinds of varieties within species are equally important as incipient species. Jordan distinguishes three kinds of such varieties, or, as he expresses it, three types of polymorphism within species : individual, seasonal and geographic polymorphism. It is interesting to note, incidentally, that there has been some recent improvement in the precision of our terminology. The term polymorphism is now applied only to variation within a population, while differences between populations are no longer included under this term. A species that breaks up into subspecies is referred to as a polytypic species and not as a polymorphic species. The clear distinction between variation within a population and between populations which we now make was not fully appreciated by Jordan. Fortunately it did not affect the validity of his argument.

Full species of insects, Jordan concludes, differ from each other in coloration and other external morphological characters and usually also in the structure of the genitalia. Incipient species then should differ from each other either in external morphological characters or in the structure of the genitalia or in both. A variety, in order to qualify as incipient species, must vary consistent with this postulate. Accordingly Jordan studied the mode of variation of the three kinds of varieties (individual, seasonal, and geographical).

Speciation by macromutation.—De Vries had recently emphasised the evolutionary importance of those individuals that lie completely outside the normal variation of a population, his so-called mutations. Such forms, Jordan says, are not infrequent among butterflies and are eagerly sought by the amateur collector. They are generally referred to as " sports ". Jordan examined the genitalia of many such sports and this is what he found (1905 : 167) : " In not a single aberration, either caught in nature or artificially produced by temperature shocks, have I found that the aberrant colouration was correlated with any differences in the genital organs. The sports remain with respect to these organs within the normal limits of variation. They are not new ' species ' which have separated themselves from the mother species by a saltation and which now could co-exist independently." It is curious how long Jordan's clear-cut refutation of De Vries' theory of speciation by mutation was ignored among the Mendelians. It is perhaps not out of place to cite in this historical survey what De Vries actually said on speciation. " The theory of mutation assumes that new species and varieties are produced from existing forms by certain leaps. The parent type itself remains unchanged throughout this process and may repeatedly give birth to new forms " (1906 : vii). " The origin of species may be seen as easily as any other phenomenon. It is only necessary to have a plant in a mutable condition " (1906 : 26). De Vries came to this viewpoint by not believing in the species of the naturalist " as Linnaeus has proposed them. These units are not really existing entities ; they have as little claim to be regarded as such as genera and family " (1906 : 12). Jordan came back repeatedly in his writings to this theory of speciation by mutation. In 1911 (p. 401) he pointed out that even polymorph types are not nearly as clear-cut as is usually maintained, provided one has sufficiently large collections. The modern geneticist might say that additional modifying factors may help to bridge the phenotypic gap between two polymorph alleles. And Jordan continues " and it is perhaps also not superfluous to reiterate in this connection that the geographical races, too, are nearly always found to be connected by intergradations, if a sufficiently large number of specimens is examined ".

Sympatric speciation.—The fact that many similar but ecologically slightly different species may occur in the same geographical area was, at an early time, interpreted as evidence for speciation without geographic isolation. One author after the other tried to discover the mechanism which would make such sympatric speciation possible. The more we learn about the co-adaptation of the gene complexes of local populations the more such schemes of sympatric speciation appear impossible. Jordan, however, without this knowledge of modern genetics had come precisely to the same conclusion merely through the study of incipient speciation and by an astonishingly lucid and logical analysis of the speciation process. Although he had disproved sympatric speciation quite conclusively in 1896, he came back to it whenever a new paper was published which tried to revive the dead theory. Those who postulated such a process with the help of the hypothesis of homogamy (the mating of the most similar individuals within a population) he countered by stating that the observations on which these claims were based were ambiguous, if not mistaken, and that even if homogamy occurred it could not lead to a splitting of a single population into two (1905 : 173). When H. M. Vernon (1897) proposed a new version of this theory entitled evolution by " Reproductive Divergence," Jordan (1897, 1898) demonstrated its fallacy so conclusively that this hypothesis never again entered the biological literature. It is historically interesting that Jordan's premises are essentially the same as those that led, subsequently, to the establishment of the Hardy-Weinberg Formula. Another contemporary who had proposed a theory of sympatric speciation was Romanes (" physiological selection ") (1897), but he had already been refuted so decisively by Wallace, in his book *Darwinism* (1889), that Jordan could afford to dismiss his thesis rather summarily (1896 : 443).

The striking morphological difference sometimes found between seasonal forms of insects had lead to the establishment of still another hypothesis of sympatric speciation by some entomologists. They argued that new species might arise if these seasonal forms became more and more different. Jordan admits that seasonal variants differ from ordinary individual variants, because they frequently " . . . separate breeding communities. . . . In the species in which the first generation of mature individuals has disappeared before the next one hatches, these generations are reproductively isolated from each other as much as is one species from another " (1905 : 174). Jordan then asked himself whether or not this really could lead to species formation. He concludes finally that the odds are all against it. First of all the summer generation is normally the direct descendant of the spring generation and secondly, there is no other evidence except phenotypic difference that these are incipient species. Jordan finds the best proof for this in the variation of the genitalia. Geographical races, which are incipient species, often deviate quite markedly in the structure of the genitalia from each other while, in the case of a large number of seasonal forms investigated by him, he found only a single species (*Papilio xuthus*) in which there is even the slightest genitalic difference. There is thus no evidence that seasonal forms are incipient species (1905 : 174).

There are two authors in particular whose hypothesis of sympatric speciation Jordan rejected emphatically. One is Dahl (1889) who had outlined an imaginary case of sympatric speciation in the genus *Gonopteryx* by postulating differences of incipient food plant races. " At the time when selection sets in in Dahl's illustration there were already two ' species,' and hence the specific distinctness of the two is not the outcome of psychological selection " (1896 : 427). Dahl had failed to explain the first crucial step which can be explained only by geographical speciation. The other of his opponents was Petersen (1903) who had proposed quite a fantastic hypothesis based on blending inheritance, correlated host and mating preference, and various other improbable or actually erroneous assumptions. It is a real pleasure to read Jordan's answer (1903) with its superb knowledge of the evolutionary literature of the period and his critical emphasis on the essential points most of which he had already listed in his 1896 paper (p. 444) : " The physiological selection will, therefore, in no case result in divarication of a species into two, but the outcome of the physiological variation will be either dimorphism of the species, when both the normal and the varietal form are equally favoured in respect to the circumstances of life, or extinction of that form which is the least favoured. If however the most favourable kind of variation does not lead to the origin of a new species beside the parent one, no other variation will lead to this end. Hence we must conclude that a divarication of a species into two or more species cannot come about so long as the divergent varieties live so together that a direct or indirect intercrossing is not prevented."

His rejection of sympatric speciation is decisive. He says that there is no possibility of the origin of a new species without the help of some kind of local separation. Nor is the hypothesis of sympatric speciation needed to explain the geographical co-existence of closely related forms. Those who postulate it overlook two factors : The ability of animals for active or passive changes of their range and the time factor. In fact, says Jordan, it can be shown quite clearly in many cases that the present co-existence of two closely related species is obviously the result of a comparatively recent invasion of each others ranges (1905 : 203).

Geographic speciation.—By showing that the various schemes of sympatric speciation do not work, and that neither mutations nor individual variants nor seasonal races qualify as incipient species, Jordan prepared the way for a discussion of geographic speciation. The questions he poses are whether or not geographic races are incipient species; and whether or not the great diversity in nature can be explained as having arisen through geographic speciation.

These questions can be answered only through a study of geographic variation.

The old concept that species are fixed, invariable types was undermined particularly by the work of Wallace in the East Indian Archipelago and that of Bates in the basin of the Amazon. Bates had pointed out that a comparison of individuals of a species from different localities revealed a graded series, ranging from such slight differences that they are not worth mentioning, to such great differences that it was doubtful whether they were still conspecific. Jordan comments that (1905 : 181–182) " these grades of variability, which Bates found on the Amazon River can be found by the systematist also in Europe. It is a universally valid fact that there are all degrees between virtual identity of individuals from two areas and morphologically constant and well defined differences. A complete identity of all the individuals of a species in two localities occurs rarely, if ever. Most often that which is normal (= most frequent) at one locality, is not normal at the other. The curve of variability has shifted at the upper or lower end or at both. It also may occur that one organ remains the same and another is different or that a species is monomorph at one locality and dimorph at another."

Jordan takes this observation of geographic variability as his starting point and asks next whether it affects only unimportant, superficial characteristics or also those which distinguish good species. It was this question in particular which induced him to undertake his historical researches in the geographic variation of genitalic structures in Lepidoptera (1896, 1905). As a conclusion of his researches he states that since many geographic races of butterflies differ from each other in the structure of their genitalia in the same manner as good species and since such geographic races vary also in all the other characters of colour and structure which distinguish species, it must be concluded that geographic races are to be considered incipient species. He continues to point out that the various characters of a species may be independent in their geographic variation. Two subspecies, which differ in colouration or wing venation, do not necessarily differ in their genitalia, the more so since even a certain number of good species is not distinguishable on this basis. The conclusion that species originate by geographic variation can be extended by analogy to animals other than insects. Jordan says that one must apply the same method to other species characters where species do not differ in the structure of the genitalia. This had been done already by Wagner, Seebohm, Hartert, Rothschild and others.

Jordan was not satisfied merely to point out the fact of geographic variation, but attempted to establish general laws governing this phenomenon. We mentioned already his discovery of the independence of different organs with respect to their variation. In the African *Papilio phorcas*, for instance, specimens from the Congo agree in colouration with such from Sierra Leone, but in the structure of the genitalia with the populations from East Africa. Other rules established by Jordan are the following : The degree of geographic variation is different from species to species and even among closely related species one may be highly constant over large areas while the other is subject to a great deal of geographic differentiation. " The amount of geographic variation depends on the nature of the environment (including the living one) and on the nature of the species. But not only on these two factors. It is also obvious that two areas between which there is an active inter-change of individuals are actually only a single area for the species because the individuals of the two areas form a single inter-breeding unit as if they were co-existing in the same area. One must therefore conclude that geographic variation depends furthermore on the degree of separation of the various geographically localised interbreeding units. The degree of separation by one and the same geographic barrier in turn will be different according to the nature of the animal. What is a barrier for a terrestrial animal like a snail or flightless insect, and therefore separates various breeding communities, may not be any barrier at all for a winged animal. And finally it is easy to comprehend that the amount of time which has passed since the separation is a factor in the origin of a geographic variety " (1905 : 187). There was no other biologist in 1905 who saw and expressed the situation as clearly as did Jordan.

" That species may differ according to locality has been known to systematists as far back as the 18th Century " (1905 : 184). Jordan's major contribution to the subject has been to treat the subject quantitatively by attempting to determine the amount of geographic variation in every species of an entire group, such as the Papilios or the Sphingidae, and by being the first to extend the investigation from a few superficial characters to such internal structures as the genital armatures. His treatment of the geographic variation of genitalic structures in the species *Papilio dardanus* is still outstanding as an example of such a quantitative treatment. Even the percentage occurrence of certain variants is recorded for each population : a spine on the valve occurs in 100 per cent. of the East African specimens, in 13 per cent. of Uganda individuals and in less than 3 per cent. of those from the west coast.

As a true biologist Jordan is not satisfied merely with describing the fact of geographic speciation, he also wants to determine its causes. Wagner, the founder of the theory of geographic speciation, had claimed that isolation in itself is an active factor of trans-mutation. This is rejected by Jordan (1896 : 445) : " Isolation as such is not an active factor which produces a character but is a factor which merely preserves a character produced by some other factor ; isolation has, therefore, no direct effects." In support of this conclusion he cites numerous facts. How can isolation itself account for the phenomenon, he asks, that the butterflies and moths of Sumatra and Borneo are quite universally dark and those from Queensland pale? Since isolation itself cannot account for this . . . " there is only one way possible by which the divarication of a species into two or more can come about—that is, the combination of isolation and transmuting factors " (1896 : 446). I believe that with this statement Jordan was the first to state clearly that speciation is the joint product of mutations and isolation. Wagner had neglected one of these factors while the contemporary Mendelians and the Darwinians ignored the other. And how, asks Jordan, do these transmuting factors act during this period of isolation : " The geographical races thus produced we must assume to be first inconstant, to become more and more constant and divergent by the incessant influence of the transmuting factors, and to develop finally into a form which is so modified that it never will fuse either with the parent form or the sister forms, and that it therefore agrees with the definition of the term ' species ' " (1896 : 446). It is quite evident from the context that Jordan understood under " transmuting factors " both genetic changes and natural selection. This was written in 1896 before the birth of genetics and a certain vagueness in terminology, like "constant" or "inconstant" is excusable. The modern geneticist would speak of the development of reproductive isolating mechanisms and of the evolution of co-adapted and integrated gene complexes. What is important is that Jordan at this early date described the process of the change of geographically isolated populations just as we do to-day. As far as the nature of the genetic changes is concerned he was still on the fence, allowing even the possibility of Lamarckian changes. However, he pointed out repeatedly, and as we must admit in retrospect correctly, that this point did not really make any difference so far as the theory of speciation is concerned. In this he was far more penetrating than any of his contempories or any other author during the fifty years that followed him.

Again and again Jordan emphasised the importance of the study of geographic variation. In 1896 (p. 446) he said with respect to geographic speciation "as this kind of divarication of species is the only possible one . . . the study of localised varieties is of the greatest importance in respect to the theory of evolution; *the study of geographical races, or subspecies, or incipient species, is a study of the origin of species*." And in 1903 (p. 664) he summarised his views as follows: "Geographic variation is the basis of species formation and it alone gives the explanation for the mutual sterility of species for which one has searched in vain since Darwin's day. Spatial separation alone permits the gradual divergence in morphology and physiology. It alone can prevent fusion with parental and sister populations of the varieties which develop in a new environment and become gradually constant. This permits that the originally very small, unimportant and inconstant differences in genitalia and other characters increase by accumulation to such an extent that a fusion is no longer possible."

Although the taxonomist normally works with morphological characters, it is evident from this quotation and from Jordan's other writings how highly he ranked physiological characters in the speciation process. "For us systematists that kind of psychological variation is of more [= greatest] interest which is the immediate outcome of morphological differences in the organs of sense and in the organs which are destined to affect the senses" (1896 : 434). In view of the fact that males discriminate between the scent of females of their own species and that of other species it should be important to look for geographic variation in this character. One such case, he continues, has already been found, namely that of Standfuss on geographic variation in smell preference between Swiss and Italian individuals of *Callimorpha* [= *Panaxia*] *dominula*. This, he says, proves how potent a factor in speciation a geographic variation in scent preference would be (1896 : 434). The relatively greater constancy of colouration in a given population of birds as compared to the much greater variability of most butterflies is due to the fact that the visual sense is the primary sense in birds while in most insects it is the olfactory sense.

Factors of Evolution.

A study of this problem shows where the principal advance in concepts has occurred since the turn of the century. The rôle of the environment was not yet clearly analysed at that time. Nothing was known as to the nature of genetic factors. Jordan was a firm believer in natural selection, but was in doubt as to its precise rôle. Again and again he comes back to the great importance of natural selection in the evolutionary process. This is particularly evident in his repeated discussions of mimicry (1897*a*, 1897*b* and 1911). " . . . There is here no difficulty at all for the theory of natural selection. The theory offers a very simple explanation by assuming that the variable ancestor of the mimicking species has been gradually modified into a di- or polymorphic species by the weeding out of those intermediate forms which did not resemble protected species already existing in the country. The frequent rarity of intermediates is direct evidence for this theory " (1911 : 403). He continues to say that this theory is not in conflict with other theories dealing with the origin of variation itself and those which interpret adaptation to local environment. Jordan then presents in full detail the genetic theory of mimetic polymorphism which has since been adopted by the majority of geneticists.

How far ahead of his contemporaries Jordan was in his thinking on natural selection is evident from two notes on mimicry he published in 1897 in *Nature*. In order to account for the usual rarity of mimics as compared to the models some students of mimicry had advanced the exceedingly anthropomorphic explanation that mimics are rare, because it is to their advantage to be rare in order that the predators will not become conditioned to them. This explanation which, as a matter of fact, is still maintained in much of the current literature, does not provide for a genetic mechanism as was clearly realised by Jordan. Instead he advanced a theory which—anticipating the recent selection experiments of Mather, Lerner, and others—has a remarkably modern ring. If the mimic " for instance, *Papilio alcidinus*, has acquired that wonderful similarity in colour and form to its model, an Uraniid moth, in consequence of a continued selection in the one direction, it is obvious that the result of such a one-sided selection will not only be similarity to the immune model, but also physiological one-sidedness. The more rigorous the selection is, the better will the mimetic species become adapted to its model, and the more it will lose its adaptability to new biological factors. . . . Consequently, the most striking 'mimics,' in spite of, or rather in consequence of, the resemblance to immune species, are, in the long run, the less favoured in the struggle for existence, which means that they will become relatively scarce. From this consideration it is apparent to me that the selection of those specimens which are the very fittest in any *special* direction is in itself a danger to the species, and can lead to destruction " (1897*a* : 153). This was written at a time when natural selection was being attacked by environmentalists and mutationists alike. Almost fifty years have passed by before the analysis of gene complexes by Mather and others have led to a genetic confirmation of Jordan's views of the detrimental effects of one-sided selection.

In 1905 (pp. 205–209) he once more tried to analyse the causes of speciation. His analysis largely leads him to reject various erroneous theories without permitting a constructive answer on the basis of the genetic facts known at that time. " The morphological facts on which we have based our conclusions give us unfortunately only the above negative answers to our question which factor or which aggregate of factors produces the difference between subspecies and species : that which better adapts an individual for the West African environment is not a selection of specimens according to a special wing pattern or according to a shift or shortening of spurs or crests on the genital valves ;

it is not the direct effect of humidity or temperature on wings or genital organs nor the release of latent characters by such factors" (1905: 209). He was willing to wait for the eventual solution with an open mind.

CONCLUSIONS.

The preceding discussion makes use of only a small portion of Jordan's life work as presented in his early major publications. Yet I believe it is enough to show that by and large Jordan was far ahead of his times, sometimes by as much as fifty years, and that in his writings and through his contacts he exerted an influence on the development of the new systematics and on evolutionary thought that cannot be over-estimated. Even though Jordan's name may not be cited as widely in textbooks of evolution and zoological systematics as it deserves, at least he has the satisfaction that most of the concepts which he pioneered and for which he fought have now been accepted by virtually every worker in the field. As one of those who have benefited from Jordan's efforts to clarify evolutionary thought and to enhance the prestige of systematics I want to record on this occasion my feeling of immense gratitude.

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1916, Jordan, K. Notes on Arctiidae. *Novit. zool.* **23** : 124–150. Besides being an excellent revisionary study, this paper concludes with probably the first clear statement of the subject of sympatry and allopatry in their relation to systematics, apparently overlooked hitherto, due to the deceptive title. *Editor.*

KARL JORDAN'S CONTRIBUTION TO OUR KNOWLEDGE OF THE ANTHRIBID BEETLES.

By Elwood C. Zimmerman.

Dr. Jordan began writing about Anthribidae in 1894. His attention was first drawn to this family of "long-horned" weevils in 1893 while he was curating and determining the Walter Rothschild collection of Coleoptera. The great morphological diversity displayed by the multitudes of tropical Anthribidae stimulated his interest to such a degree that he has worked on the family for the past 62 years—that is, whenever he could take time away from being a world's authority on fleas, butterflies, hawk moths, evolution and other subjects, besides being one of the world's most international and catholic entomologists!

Dr. Jordan has written about 145 papers on anthribids, and in these reports he has described about 150 genera and 1900 species and subspecies. He has described nearly 45 per cent. of the known genera and over 65 per cent. of the known species of Anthribidae. In the past quarter of a century he has described about seven times as many genera as all the other workers on Anthribidae combined. He has told me that he looks upon all his naming and describing as "elementary and preliminary but essential", and that "It would have saved us taxonomists a lot of trouble if Noah had imprinted an inheritable name on the bodies of the millions of species he prevented from becoming extinct by drowning."

The amalgamation of Karl Jordan's collection of some 22,000 specimens (which is gradually being accomplished) with that of the British Museum will result in a combined collection of far greater value than the combined collections of all of the museums of the world. Hardly any described genera and only a few of the known species are lacking from this great collection, which contains about 75 per cent. of the holotypes of the world's Anthribidae, including those of Jordan, Pascoe, Sharp, Wollaston, Jekel and Broun.

In 1906, when Jordan contributed his monograph to the *Biologia Centrali-Americana* he raised the number of known Anthribidae from that tropical American wonderland from about 35 to nearly 200. Only a half dozen or so anthribids have been added to the Central American faunal list since Jordan's work was published half a century ago, in spite of the fact that his monograph includes keys to all the genera, and species, and almost every species is illustrated, thus giving other workers a very clear picture of the fauna and forming an unusually sound base for future work. Now, at the age of 93, he is at work on a generic revision of the Anthribidae to crown his monumental contributions.

It is superfluous to say that no other man has contributed so much to our understanding of the Anthribidae as has Dr. Jordan. He has entered unknown fields and has revealed the natural richness of many faunas to his fellow men.

Jordan is truly a man of extraordinary ability and accomplishment. His powers of observation, reasoning and interpretation have been developed to an astonishing degree of acuteness. His knowledge of general entomology is profound. He is a man who has been able to see the trees as well as the forest.

He has never let the mass of new species he has worked with befog his overall thinking, nor has he let " species making " become an end in itself. He has always been looking for the new, the unusual, the bits and pieces of evidence which would supply him with material to add weight to, or clarify, theories and problems in evolution and other fields. The unusual markings on this or that anthribid have not just been passed over as interesting spots, but he has sought the " why " of the maculae. He always wants to know why the animal has become so coloured or so formed or so ornamented and what relation these features have to its environment and to its associates. When he has an anthribid under his microscope he pictures the specimen as it might appear resting on an epiphyte-covered tree trunk in a tropical jungle where its markings conceal it from the eager eyes of hungry birds. He wants to know why it is that the hereditary factors which control the production of certain characters on the outer sides of the mid and hind legs of an anthribid reverse themselves and produce the same characters on the inner sides of the front legs of the same individual. He inquires as to why several species in non-related genera develop extraordinary, complex, almost identical color patterns. These are the kinds of things to which his mind is ever alert. These are the kinds of things which mean much to him on his journeys in systematics through the jungles of species with which he works.

Jordan is a genius, the like of which appears only as an extraordinary, rare and fortuitous circumstance in time. We have had few such minds in entomology. Such men cannot be produced by the will of men—they are the gift of Nature, perhaps placed among the lesser of us as examples of the goals of good and accomplishment we can strive for.

Vir eminentissime, Nestor artis entomologicae, qui per tot annos singulari ardore insectorum studio te dedisti ; qui operibus tuis eruditissimis summaque elegantia confectis scientiam naturalem adornasti, nos, amici tui atque eiusdem disciplinae consortes, ab imis medullis te salutamus !

KARL JORDAN THE LEPIDOPTERIST.[1]

By Eugene Munroe.[2]

(*Systematic Entomology Unit, Entomology Division, Ottawa, Canada*).

Karl Jordan became interested in Lepidoptera at an early date: his first published work was his doctoral thesis on the lepidopterous fauna of Göttingen (1885). This was followed by a more extensive work on the Lepidoptera of north-western Germany (1886), but in the immediately following years Jordan's attention was evidently turning more and more towards Coleoptera, and had he not gone to the Tring Museum as Curator of Insects it is doubtful whether his work in Lepidoptera would have been extensive.

At Tring, too, Jordan's research was at first concentrated on beetles, as several important papers in Volume I of *Novitates Zoologicae* attest. It was not until Walter Rothschild began intensive work on the Indo-Australian Papilios that he found it necessary (as he explains on the first page of his paper on that subject) to call on Jordan, in his capacity as Entomologist of the Tring Museum, to carry out much of the time-consuming bibliographic, anatomical and other technical work required as preparation for an adequate treatment. The results of Jordan's studies were partly embodied in the fine descriptive text prepared by Rothschild, and partly expressed in a number of short initialled notes dispersed through the paper and in a longer introductory passage, unsigned, but with Jordan's authorship indicated by Rothschild in his prefaratory remarks.

In these early notes the hand of the master is already evident. It is hard now to apportion credit for ideas that must have matured in long hours of discussion in that eager and superbly endowed Tring environment of the 'nineties; certain it is that in Jordan's writings of this and immediately subsequent years there is a firm exposition of general principles and an obvious command of basic taxonomic concepts for which we search in vain in the works of his colleagues and contemporaries. Jordan's notes on *Papilio*, written ten years before the rediscovery of Mendel's laws, and forty years before the modern synthesis of taxonomy and population genetics, can be read virtually without reservation to-day. Here we find emphasis on the importance of series and, more, of adequate samples from every part of the geographic range. Here is a worker in possession of hitherto unrivalled material, who might well have been excused a touch of complacency, but who instead borrows specimens from almost every important collection, and bemoans the inadequacy of the accumulated resources of the world. Here, too, we find a clear understanding of the importance of types as standards of identification; here is a perfectly modern concept of the population as the basic unit in taxonomy, and a clear relegation of environmental and individual variation to a subordinate place; here is recognition of the plasticity and local variation that exist within larger and more definitely characterised populations; here are a mature appreciation of the process of geographic speciation, a firm and definite subspecies concept, and a recognition of the importance of vicarious species. These clear ideas are reflected in an equally clear nomenclatorial practice: the trinomen is explicitly reserved for the subspecies; indeed we find Jordan urging the taxonomic co-ordinacy of the nominate subspecies with other subspecies, and its nomenclatorial treatment as a trinomen, on his as yet reluctant co-editors, Rothschild and Hartert! Yet all this remarkable distillation is contained in an incidental passage of fourteen pages inserted in another author's paper. Coupled as it is with abundant evidence of a deep and comprehensive insight in the detailed taxonomic treatment, this essay is an impressive portent of things to come.

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The interest thus aroused in exotic Lepidoptera rapidly extended into broader fields, and we soon find Jordan standing at Rothschild's shoulder in a wide variety of lepidopterological enterprises. In the first line stood the projected series of comprehensive monographs of special families or groups. To the history of this we shall refer in due course. This major concern was supplemented by a number of smaller independent or corollary investigations, and the years 1895 to 1903 yielded eleven taxonomic papers on miscellaneous groups of Lepidoptera, as well as two fundamental studies of the morphology of the order and four papers on evolution in which data drawn from Lepidoptera played an important part. All this was in a period of continuous productivity in the study of Coleoptera, a period in which also the later very important interest in fleas was awakened, and in which two monographs—of *Charaxes* and allies and of the Sphingidae—were completed. The sheer volume of this output—about 2000 pages, in addition to many hundreds of drawings and much work on papers written by other authors—is sufficiently impressive, but when the high degree of originality and the almost unique depth and accuracy of the work are realised, the magnitude of the achievement becomes fully apparent.

The various short taxonomic papers on butterflies and moths, though of uniformly high technical quality, are useful principally to the specialist. The morphological papers, however, are of more general interest and display remarkable originality. The long paper on the structure of butterfly antennae is a comprehensive investigation and synthetic treatment of the subject far surpassing any that had preceded it, or indeed any that has followed. Four principal organ-systems were studied, chosen for ease of observation and convenience as taxonomic characters. These were: the scales, the fine sense-hairs, the setiferous punctures, and the sense-bristles. The wise restriction to easily observed characters and the already large scope of the Tring collection allowed Jordan to examine the antennae of thousands of species, including many rare or isolated ones. From such extensive material previously unsuspected regularities readily emerged. In his account, Jordan first synoptically discusses the structures found in the different families. The characteristic thoroughness and accuracy of this section is illumined by flashes of remarkable insight: the fundamental cleavage of the Pieridae is recognised, and *Leptidea* is associated with the Dismorphiinae; *Styx* is correctly placed in the Erycinidae and *Pseudopontia* in the Pieridae; the anomalous position of *Pierella* is hinted at, and the discussion of the Papilionidae foreshadows the definitive classification to be outlined eight years later. The detailed treatment of families is followed by a typical synthetic section, scholarly and informative, in which the classification of the butterflies and their relationship to the moths are discussed at length.

Even to-day there is no agreement on the definitive classification of the butterflies, but Jordan's paper will remain an important contribution to the literature of the subject.

The paper on the mesosternum is shorter and less elaborate than that on the antennae, but shows the same search for new sources of taxonomic characters, a search that is typical of all Jordan's work. Here the early background in Coleoptera suggests the potential importance of the scale-covered thoracic sclerites, which are studied with characteristic thoroughness and accurate attention to detail. Although sclerites are included that would be considered pleural by modern morphologists, the basic elements are clearly recognised, and salient features of the taxonomic groups are pointed out. Again there is the characteristic synthesis, with emphasis on phylogeny and on the placement of aberrant forms; once again there is a sustained effort to weigh resemblances and differences, and to distinguish between primary affinities and secondary or convergent similarities.

Two papers of this period bearing on general evolutionary questions are of particular interest to lepidopterists. The first is the large paper *On Mechanical Selection and Other Problems* (1896). The section dealing with mechanical selection in Papilionidae and other butterflies is actually a comparatively small part of this long essay. The principle of mechanical selection has been adversely criticised by some subsequent authors, but it is doubtful if the criticism has been based on anything approaching the morphological and biological knowledge of Papilionidae that was marshalled by Jordan in support of his theme. Indeed, the correspondence between structural specialisations of male and female in Papilionidae and in some other groups of Lepidoptera is so intimate that we may well find it hard to believe that selection does not in fact operate to maintain it. However, of far more interest than the details of the hypothesis advanced is the development of the large and varied array of supporting evidence. Characteristically, Jordan unites broad and often original theoretical considerations with a wealth of new morphological data, forming an argument rich in both facts and ideas. First there is a discussion of the species concept in the light of polymorphism, heredity and geographic variation, which, particularly considering its date, is remarkable for balance and acuity. Then comes the long detailed section on male and female genitalia of *Papilio*, with a wealth of new descriptions and illustrations of these previously little-known structures. This leads naturally to a discussion of the striking and then new facts of geographic and individual variation in these organs, with digressions on the zoogeography of the Malayan Archipelago. Outmoded as some of the theoretical side of this paper now is, there remains a wealth of fascinating reading in the supporting data alone, while the main hypothesis of mechanical selection is backed by circumstantial evidence for which any other explanation is still lacking.

The second paper dealing with evolutionary questions largely on the basis of evidence drawn from Lepidoptera is the critique of Eimer's *Orthogenesis der Schmetterlinge* (1898). This makes an interesting contrast with the paper on sexual selection, being as remarkable an example of destructive dialectic as the latter is of synthetic reasoning and exposition. Although the material does not go beyond a defence of statements previously attacked by Eimer, the many weaknesses of the evidence on which Eimer based his rather rash criticisms are fully and convincingly exposed. This essay can still be recommended as salutory reading for those tempted to publish without due prior reflection.

We must now return to the series of large monographs of lepidopterous groups. The first to be published with Jordan as a full co-author was the *Monograph of* Charaxes *and the Allied Prionopterous Genera* (1898–1903). This paper was issued in four parts. Its scale is lavish: 381 pages, 17 plates, and numerous photographs and line-drawings in the text are devoted to a group of only 121 species. As might be expected, the treatment shows a considerable advance over that in the revision of the eastern *Papilios*. The range of anatomical characters studied is much wider; interesting notes are given on the structure of legs, wings, and genitalia, and the modifications of these organs are carefully studied throughout. The descriptions are fuller and more consistent, and are supplemented by numerous half-tones and coloured illustrations of whole insects. The trachea-based system of naming the wing-veins is used, as it was in the *Papilio* revision, but here a brief description is given, and attention is called to the special features found in *Charaxes* and allies. There is much more attention to life-histories and to seasonal and ethological data, and the importance of field observation and study is again and again stressed.

The problems in this group are different, and in some respects more refractory, than those that were encountered in the Oriental *Papilios*. There are intricate and previously hardly understood examples of sex-limited polymorphism, complicated in one case by a close parallelism between polymorphism in different species. Genitalia and other anatomical features are much less revealing than in most Papilionidae, and there are several arrays of deceptively similar but specifically different forms. Jordan's insight proved equal to these difficulties, and though the classification of *Charaxes* has been amplified and refined with increasing knowledge, it has suffered comparatively little change, and that mainly in the detailed classification of the most obscure groups.

In 1903 appeared the culmination of this series of monographs, the Rothschild and Jordan *Revision of the Lepidopterous Family Sphingidae*. This noble work was published as a supplement to Volume 9 of *Novitates Zoologicae*, and therefore did not suffer from an awkward division into instalments, as did the *Charaxes* revision.

The revision of the Sphingidae is possibly the finest example of a taxonomic monograph that has ever been produced in Lepidoptera: it is well worthy of the striking insects that form its subject. In plan this revision is what is so rare in taxonomic work, a balanced and detailed study of the classification of a whole group from the world standpoint. The general introduction, of 135 pages, is, as usual in Jordan's work, of fascinating interest, and is characterised by balance, accuracy and attention to detail. A few pages deal with the history of the study of Sphingidae and with this project in particular; once again we see that the authors have been at pains to examine all available material, a radical attitude at that time, when the collection was still often considered more important than the work. A summary of principles of nomenclature is given. These principles unfortunately do not always agree with the International Rules as now constituted; however, Rothschild and Jordan's rules are simple, logical, clearly stated and consistently followed. Without the gift of second sight the authors could hardly have been expected to achieve more. The rather detailed section on the principles of classification has a surprisingly modern ring. I can well remember the strong impression this passage made on me when I first read it. Even to-day, with so much good and modern literature on taxonomic method available, Rothschild and Jordan's remarks, the fruit of wide and successful practical experience, can no doubt be studied with profit by the commencing taxonomist.

The fifty-odd pages on the morphology of Sphingidae, accompanied by more than fifty plates figuring anatomical detail, are striking evidence of the patient search for taxonomic characters that is the foundation of Jordan's methodology. Once again the technique is far ahead of its time, for almost all lepidopterists of that day relied on colour and pattern, supplemented by only the crudest morphological differentiae. The morphological section is followed by a summary of geographical distribution. Once again detailed data are marshalled in support of clear and definite arguments. Some of the paleogeographic conclusions do not agree well with modern theory, but one must remember that far less was known of geological processes and history fifty years ago, and that reconstructions that seem obviously suspect to-day were perfectly orthodox at that time. The general emphasis on the normal, rather than the erratic, distribution is extremely sound, and the zoogeographic account as a whole is an accurate conspectus of the distribution of one of the comparatively well-known animal groups.

The main defect of the taxonomic section is that a number of names must be changed or used in different senses to accord with present rules of nomenclature. Although this was hardly the fault of the authors, it does tend to reduce the convenience of the monograph for present use. However, this minor blemish is far overshadowed by the technical quality of the work itself. Subfamilies, genera, species and subspecies are described in meticulous detail on the basis of the best material available at that time. Although not every taxonomic conclusion in this thousand-page work has withstood the revisions and discoveries of fifty years, the general classificatory structure remains unchanged. A few authors have questioned the separation of Sesiinae and Philampelinae, but it is doubtful if the criticisms have been based on as thorough study as was the original arrangement. Keys are provided throughout, genitalic and other structural characters are lavishly illustrated, and figures of the whole insect are given for many rare or obscure forms. A special feature of the work are the phylogenetic diagrams, in which not only are the hypothetical relationships shown, but a summary is given for each genus of the characters that lead to its assignment to that particular position.

The revision of the Sphingidae is a model for taxonomic investigation and writing. Its continuing usefulness exemplifies the value of thorough, balanced, synthetic study of an entire group in minimising the inevitable instability of taxonomic work.

This revision in a sense marked the culmination of Jordan's career as a lepidopterist. External factors caused the progress of the great monographs to be first slowed, then halted. Although a very large amount of useful work lay ahead, nothing on quite the same scale was ever again completed in Lepidoptera, and interest shifted more and more to other groups as years progressed.

Three important monographs appeared after the revision of the Sphingidae. The first was the Rothschild and Jordan *Revision of the American* Papilios (1906).

Although just as detailed and informative on the species level as the sphingid monograph, this revision contains far less material of a general nature. Most of the authors' fundamental views on taxonomic principles had already been discussed in the introduction to the sphingid paper only three years earlier. Furthermore, as a subsequent generic revision of the Papilionidae was at that time planned, characterisation of supra-specific categories was reduced to a bare minimum. Unfortunately this projected revision never appeared. The detailed accounts of the American swallowtails are, however, interesting and useful in the extreme. Order was introduced into a previously chaotic group, and a definitive classification was established, to which there have been only a handful of additions in forty-nine years. The illustrations of adult insects are of the usual high quality, though they are perhaps less numerous than could be wished. Early stages and genitalia are briefly described but unfortunately not figured.

The other two revisions were much later, but once again were planned as integral parts of a larger work, a monograph of the Saturnioidea. These works are the *Monograph of the Saturnian Subfamily Ludiinae* and *On the Saturnioidean Families Oxytenidae and Cercophanidae.* The three groups revised are each small, but of great interest because of their combination of specialised and primitive features. These groups differ from those considered in the earlier monographs in that none is either really abundant or an established favourite of collectors. The available material, therefore, was not nearly so comprehensive, and further interesting discoveries undoubtedly remain to be made. However, the treatment is characteristically thorough and sound, and almost all the known species are figured as well as being described.

Another important group of contributions are sections in such works as Seitz' *Macrolepidoptera of the World*, Junk's *Lepidopterorum Catalogus*, and Wytsman's *Genera Insectorum.* In the years 1907 to 1916 Jordan, alone or with Rothschild, prepared fourteen such contributions, dealing with six families of butterflies and moths and four major faunal regions. Some of the contributions, notably the Palaearctic Saturniidae and the Indo-Australian Papilionidae in Seitz, represent a marked advance over previous publications in the same field. All are of the usual high standard, and contrast agreeably with the hack work that has tended to creep into such compiled universal works.

In addition to these large studies, Jordan has published since the appearance of the revision of the Sphingidae over 100 descriptive papers of varying lengths on Lepidoptera, and more than twenty papers dealing with special aspects of lepidopterous morphology and biology. Many striking forms and interesting problems are discussed in these publications. Perhaps the most interesting is the paper on mimetic Lepidoptera presented at the First International Congress of Entomology (1911). The bold predictions as to the conspecificity of certain strikingly different forms of *Pseudacraea* were brilliantly verified by Carpenter's breeding experiments in Uganda a few years later.

Jordan's most recent paper on Lepidoptera is the account of the Sphingidae of the Oxford University Cayman Islands Expedition (1941). That his interest in the group has not lapsed is, however, shown by his stimulating presidential address to the Lepidopterists' Society, delivered as late as 1953.

Unique though Jordan's published work is, it is not his only important contribution to the study of Lepidoptera. Elsewhere in this volume the story of his work in nomenclature and in the general biological sphere is told. These activities have had important consequences for lepidopterists, but they need not be detailed here. However, I cannot close without some mention of Jordan's part in forming the enormous Lepidoptera collections at the Tring Museum. These collections will be an abiding monument to the energy and foresight of the late Lord Rothschild, but their detailed composition—the balance, the wide and thorough geographic and taxonomic representation, and above all the long and representative series from as many localities as possible—show clearly the effects of Jordan's careful planning and supervision over many years. Not content merely to amass material, Rothschild and Jordan stimulated the ablest professional collectors of the time to explore important and previously uninvestigated territories. The results are evident to anyone who knows the Tring collection. Particularly in Oriental and Papuan material this collection is virtually unrivalled, and because of its representative nature and intelligent assembly it is one of the most satisfactory in the world from the research standpoint.

Quite aside from Jordan's scholarly attainments, his generosity and courtesy to other lepidopterists has had a strong influence on the profession. As noted above, at a time when individual work and jealous guarding of material sometimes seemed almost the rule, Jordan was advocating and practising a broadly co-operative approach to taxonomy. The large collections at Tring were never a sufficient basis for his studies : he fully realised the inadequacy of the assembled collections of the world.

His personal kindliness harmonises with these liberal principles. I remember well my first visit to Tring, some years ago. I came young, unknown and unannounced. Yet the great Lord Rothschild and the eminent Dr. Jordan did not find it too much to spend an afternoon with the inexperienced youth, and patiently to show him a part of their collections. The impression was indelible. This small incident is typical of hundreds of gestures during a long and influential career. In all parts of the world there are lepidopterists whose work has been immeasurably stimulated or helped by contact, personal or in correspondence, with Jordan.

Sometimes genius remains unrecognised in its own time. Happily this was not the case with Karl Jordan. His ability was already acclaimed half a century ago. It was his good fortune to encounter facilities and circumstances peculiarly adapted to his talents, and to exercise them unremittingly during a long, respected and still active career. As his successors and debtors let us wish him well.

" Since Linné applied the term *varietas* to the forms which are not specifically different, we do not see any reason against the use of this very convenient word in the same sense for all the components of a species which differ from one another. We understand, therefore, under *variety* not a particular category of the components of a species, but employ the term for all the different Members of a species indiscriminately. The different categories of varieties must receive special terms in a precise classification, and special formulae must be employed for them in a precise nomenclature.

" We distinguish three categories of varieties, namely :—

I. *Individual variety.*—The following terms are employed by us :

(1) *ab.* = *aberratio* for individuals which stand outside the normal range of variation.
(2) *f.* = *forma* in the case of di- and polymorphism. If a form occurs rarely, it may be termed *f.ab.*, in contra-distinction to *f.norm.*
(3) ♂-*f.* or ♀-*f.*, if the respective form belongs to one sex only.
(4) *f.loc* = *forma alicuius loci*, if in the case of polymorphism, a form is restricted to one portion of the range of the respective variety or species.

II. *Generatory variety.*—This variety is seasonal in Lepidoptera, and is designated as

(5) *f.t.* = *forma tempestatis.*

III. *Geographical variety or subspecies.*—This is the highest category of varieties. As the term *varietas* includes also other varieties, it cannot be employed as such for the geographical variety except in a precise nomenclature ; either a specifying attribute must be added (*var. geogr.*), or an abbreviation of another term chosen (*subsp.*). But we do not see that it is at all necessary to put any such abbreviation of a term before the subspecific name. We can do without the encumbrance of the abbreviation—what we can do without is unnecessary ; and is an unnecessary encumbrance in nomenclature, common-sense compels us to drop—by

(6) Simply mutually agreeing that a subspecies is designated by its name added to that of the species without any abbreviation before the subspecific name. This means *simplification of nomenclature, nothing else.*"

(Jordan, K., 1903, *Novit. zool.* **9** (Suppl : xliii.)

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BIBLIOGRAPHY OF SCIENTIFIC PUBLICATIONS BY H. E. K. JORDAN.

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Compiled by G. H. E. Hopkins.

In making the following list of Dr. Jordan's publications a difficulty has arisen with regard to papers published in collaboration with others, since his name does not invariably appear as an author of work to which he made a substantial contribution. *A revision of the Papilios of the eastern hemisphere, exclusive of Africa*, for instance (1895, *Novit. zool.* **2** : 167–463), not only contains (p. 167) an acknowledgment of a great deal of assistance from him, but also (p. 168) an unassimilated section in which reference is made to " when I began to study the Papilios more closely under Mr. Walter Rothschild's guidance ", but the fact that it was published under the sole authorship of the latter might have compelled us to omit this very important item but for the fortunate fact than many of the footnotes are signed " K. J.". Similarly, the late Lord Rothschild's presidential address to the zoological section of the British Association is known to have been largely inspired by Dr. Jordan. But Dr. Jordan's generosity in permitting his correspondents to make use of facts contributed by him means that to include in the bibliography such clear instances as that last mentioned would open the door to hosts of others in which a decision might be extremely difficult, while to trace them all would be practically impossible. In these circumstances the bibliography has been rigidly confined to works in which Dr. Jordan's name appears as author or part-author, except that the existence of the signed footnotes and the importance of the item have caused us to make a unique exception in favour of the revision of the Papilios.

A few of the more recent items were signed with the name H. E. K. Jordan[1], but in all the earlier ones the author's name is given as K. Jordan. Joint papers with W. Rothschild have the latter as senior author with a single exception (1895, Some new forms of the genera *Bizarda* and *Milionia*) ; joint papers with N. C. Rothschild invariably have the latter as junior author.

1885. *Die Schmetterlingsfauna Göttingens*, pp. vi + 52 + (1). Alfeld. (Inaug Dissert. Erlangung der phil. Doctorwürde Univ. Göttingen.)

1886. Die Schmetterlingsfauna Nordwest-Deutschlands. *Zool. Jb.* Suppl. **1** : i–xviii, 1–164.

1886. Nachtrag zum Verzeichniss der Käfer Hildesheims. *Societas entomologica Zürich* **1** : 121, 130, 139, 145, 154, 161, 172, 179.

1887. Nachtrag zum Verzeichniss der Käfer Hildesheims. *Societas entomologica, Zürich* **2** : 4, 20, 29, 60, 73, 83, 178, 185.

1888. Nachtrag zum Käfer-Verzeichniss Hildesheims. *Societas entomologica, Zürich* **3** : 1–2, 11, 21, 58, 65.

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[1] Heinrich Ernst Karl. Dr. Jordan sometimes used these initials in correspondence as well as in publications, instead of the more familiar K. J.

1888. Anatomie und Biologie der Physapoda. *Z. wiss. Zool.* **47** : 541–620, pls. 36–38.

1893 (with W. Rothschild). On two new species of the genus *Enoplotrupes*, Lucas. *Ann. Mag. nat. Hist.* (6) **12** : 36–38.
1893 (with W. Rothschild). On some new or little-known species of Coleoptera from the East. *Ann. Mag. nat. Hist.* (6) **12** : 452–455.
1893 (with W. Rothschild). Two new species of Lepidoptera from German New Guinea. *Ann. Mag. nat. Hist.* (6) **12** : 455–457.

1894. New species of Coleoptera from the Indo- and Austro-Malayan Region, collected by William Doherty. *Novit. zool.* **1** : 104–122, pl. 8, figs. 1–10.
1894. New species of the genus *Scymnus* Kugel. from the east and New Guinea. *Novit. zool.* **1** : 122–138, pl. 8, figs. 11–21.
1894. On African Longicornia. *Novit. zool.* **1** : 139–266, pls. 9, 10.
1894. On some new genera and species of Coleoptera in the Tring Museum. *Novit. zool.* **1** : 484–503, pl. 13.
1894 (with W. Rothschild). Six new species of *Plusiotis* and one new *Anoplostethus*. *Novit. zool.* **1** : 504–507.
1894. On Anthribidae in the museum of the Honourable Walter Rothschild. *Novit. zool.* **1** : 591–651.
1894. On a new species of *Cicindela* from Luzon. *Novit. zool.* **1** : 663.
1894. Two new species of Cetonidae. *Novit. zool.* **1** : 691, 692.

1895. On some new species of Coleoptera in the museum of the Hon. W. Rothschild. *Ann. Mag. nat. Hist.* (6) **15** : 218–223.
1895. Beitrag zur Kenntniss der Anthribidae, II. *Stettin. ent. Ztg* **56** : 122–204.
1895. Zur Kenntniss der Anthribidae. III. *Stettin. ent. Ztg* **56** : 245–265.
1895. Einige neue Käfer der Indo-Australischen Region in der Sammlung des Trings-Museums. *Stettin. ent. Ztg* **56** : 266–271.
1895. (Notes in : W. Rothschild. A revision of the *Papilios* of the eastern hemisphere, exclusive of Africa. *Novit. zool.* **2** : 167–463, pl. 6.)[2]
1895 (with W. Rothschild). Some new forms of the genera *Bizarda* and *Milionia*. *Novit. zool.* **2** : 464, 465.
1895. Zwei neue Lamiinen aus West-Afrika. *Stettin. ent. Ztg* **56** : 367, 368.
1895. Zur Kenntniss der Anthribidae, IV. *Stettin. ent. Ztg* **56** : 369–401.

1896 (with W. Rothschild). Notes on Heterocera, with descriptions of new genera and species. *Novit. zool.* **3** : 21–62, 185–208, pl. 4.
1896. On mechanical selection and other problems. *Novit. zool.* **3** : 426–525, pls. 16–19.

1897. Anthribidae from the islands of Engano, Mentawei and Sumatra, collected by Dr. E. Modigliani. *Ann. Mus. Stor. nat. Genova* **38** : 623–643.
1897. On mimicry. *Nature, Lond.* **56** : 153, 419.
1897. Some new Anthribidae in the Tring Museum. *Novit. zool.* **4** : 173–177.

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[2] Many of the notes in this paper are signed "K. J.". It is obvious from internal evidence that a long introductory passage on pp. 168–182 is also by him and it is credited to him (not very clearly) by W. Rothschild at the bottom of p. 167. This introductory passage is of importance as Jordan's pioneer essay on methods of classification of Lepidoptera.

1897 (with W. Rothschild). Notes on Heterocera, with descriptions of new genera and species. *Novit. zool.* **4** : 314–365, pl. 4.
1897. Coleoptera. *In* A. Donaldson Smith, *Through Unknown African Countries*, Appendix I : 447–454.

1898. Reproductive divergence not a factor in the evolution of new species. *Natural Science, Lond.* **12** : 45–47.
1898. New Anthribidae. *Novit. zool.* **5** : 359–373.
1898. Contributions to the morphology of Lepidoptera. I. The antennae of butterflies. *Novit. zool.* **5** : 374–415, pls. 14, 15.
1898. Some new Coleoptera in the Tring Museum. *Novit. zool.* **5** : 419, 420.
1898. An examination of the classificatory and some other results of Eimer's researches on eastern Papilios. *Novit. zool.* **5** : 435–455.
1898 (with W. Rothschild). A monograph of *Charaxes* and the allied prionopterous genera [I]. *Novit. zool.* **5** : 545–601, 38 figs., pls. 5–14A.

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1899 (with W. Rothschild). On some new Lepidoptera from the East. *Novit. zool.* **6** : 429–444, 2 figs.

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1902. Lepidoptera Heterocera. *In* Shelford, Observations on some mimetic insects. . . . *Proc. zool. Soc. Lond.* **1902** : 274, pl. 21, fig. 12.

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1903. Some new species of moths. *Novit. zool.* **10** : 315, 316.
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1906. Two new *Xenocerus* (Anthribidae) in the collection of R. von Bennigsen. *Novit. zool.* **13** : 410.
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1912. Contribution to our knowledge of the morphology and systematics of the Polyctenidae, a family of Rhynchota parasitic on bats. *Novit. zool.* **18** : 555–579, 2 figs., pls. 12–14.
1912. On new or little-known *Delias* from New Guinea. *Novit. zool.* **18** : 580–593.
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1912. On the Geometrid genus *Eubordeta* Roths. *Novit. zool.* **18** : 596–599.
1912. A new hawk-moth from Ecuador. *Novit. zool.* **18** : 599, 600.
1912. Some new Anthribidae. *Novit. zool.* **18** : 601–604.
1912. Familie: Agaristidae. *In* Seitz, *Gross-Schmetterlinge der Erde*, Abt. 2, Bd. **11** : 1–30, pls. 1–4.
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1913. Notes on Palaearctic Zygaenidae. *Novit. zool.* **20** : 442, 443.

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1915. On *Papilio dixoni* Grose-Smith (1900) and *Papilio kuehni* Honr. (1886) from Celebes. *Novit. zool.* **22** : 270–273, 4 figs.

1915. Some new or little-known Heterocera. *Novit. zool.* **22** : 274–278, 3 figs.

1915. On the position of *Minetra nodrica* Boisd. (1832), a Nymphaline butterfly. *Novit. zool.* **22** : 279–280.

1915 (with W. Rothschild). Thirteen new Sphingidae. *Novit. zool.* **22** : 281–291, 7 figs., pl. 20 figs. 1–3.

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1915. New exotic Zygaenidae in the Tring Museum. *Novit. zool.* **22** : 295–301.

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1915 (with N. C. Rothschild). Contribution to our knowledge of American Siphonaptera. *Ectoparasites* **1** : 45–60, 17 figs.

1916 (with W. Rothschild). Corrections of and additions to our "Revision of the Sphingidae". *Novit. zool.* **23** : 115–123, 3 figs.
1916. A new species of Geometridae from New Guinea. *Novit. zool.* **23** : 123.
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1916. On the Oriental Anthribid genus *Apolecta*. *Novit. zool.* **23** : 342–349.
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1916. Anthribidae collected by Monsieur I. Vitalis de Salvaza in French Indo-China. *Novit. zool.* **23** : 359–363, 4 figs.
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1919. Some Sphingidae from the east. *Novit. zool.* **26** : 190–192, 3 figs.

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1920. The status of *Platysphinx bourkei* Trimen (1910). *Novit. zool.* **27** : 163-166.
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1921. On the replacement of a lost vein in connection with a stridulating organ in a new Agaristid moth from Madagascar, with descriptions of two new genera. *Novit. zool.* **28** : 68–74, 9 figs.
1921. Two new African Sphingidae. *Novit. zool.* **28** : 277–279, 6 figs.
1921. A link between the double and single receptacula seminis of Siphonaptera. *Ectoparasites* **1** : 127, 128, 1 fig.
1921 (with N. C. Rothschild). A new species of Sarcopsyllidae. *Ectoparasites* **1** : 131, 132, 2 figs.

1921 (with N. C. Rothschild). Four new Palaearctic *Ctenophthalmus*. *Ectoparasites* **1** : 133–137, 6 figs.
1921 (with N. C. Rothschild). Two new Palaearctic Siphonaptera. *Ectoparasites* **1** : 138–140, 3 figs.
1921. Notes on some fleas in the Genoa Museum. *Ectoparasites* **1** : 141.
1921 (with N. C. Rothschild). New genera and species of bat-fleas. *Ectoparasites* **1** : 142–162, 32 figs.
1921 (with N. C. Rothschild). Eight new *Ceratophylla*. *Ectoparasites* **1** : 163–177, 19 figs.
1921 (with N. C. Rothschild). On *Ceratophyllus fasciatus* and some allied Indian species of fleas. *Ectoparasites* **1** : 178–198, 30 figs.

1922. On a new genus and species of Polyctenidae from West Africa. *Ectoparasites* **1** : 199–203, 4 figs.
1922. The American Polyctenidae. *Ectoparasites* **1** : 204–215, 8 figs.
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1922 (with N. C. Rothschild). New Siphonaptera. *Ectoparasites* **1** : 266–283, 18 figs.
1922. Notes on the distribution of the organ of Berlese in Clinocoridae. *Ectoparasites* **1** : 284–286, 5 figs.
1922. On an organ peculiar to the females of some genera of Ludiinae, a subfamily of Saturniidae. *Novit. zool.* **29** : 247–248, 4 figs.
1922. A monograph of the Saturnian subfamily Ludiinae. *Novit. zool.* **29** : 249–326, 169 figs., pls. 1, 2.
1922. Die von G. Tessmann in Spanisch Guinea gesammelten Anthribiden, nebst Beschreibungen einiger anderer afrikanischer Arten. (Col.). *Ent. Mitt.* **11** : 131–158.
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1923 (with N. C. Rothschild). Further records of Algerian Siphonaptera. *Ectoparasites* **1** : 290–292.
1923 (with N. C. Rothschild). On some Siphonaptera from the eastern hemisphere. *Ectoparasites* **1** : 293–308, 30 figs.
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1923. The scent-organ of certain mimetic Castniidae. *Proc. ent. Soc. Lond.* **1922** : xci.
1923. On the comb-bearing flap present on the fourth abdominal segment in the males of certain Notodontidae. *Novit. zool.* **30** : 153, 154, pl. 2, figs. 9–13.
1923. On a scent-organ found on the head of many Lepidoptera. *Novit. zool.* **30** : 155–158, pl. 2, figs. 1–8.
1923. On the scent-organs in the males of certain American Castniidae. *Novit. zool.* **30** : 159–162, 7 figs.
1923. A note on the families of moths in which R^2 (= vein 5) of the forewing arises from near the centre or from above the centre of the cell. *Novit. zool.* **30** : 163–166, pl. 3.
1923. New eastern Anthribidae. *Novit. zool.* **30** : 167–185.
1923. Four new Sphingidae discovered by T. R. Bell in North Kanara. *Novit. zool.* **30** : 186–190, 10 figs.
1923. New Anthribidae from the eastern hemisphere. *Novit. zool.* **30** : 216–221.
1923. On *Anaitis efformata* Guen. (1858), a species distinct from *A. plagiata* L. (1758). *Novit. zool.* **30** : 243–246, 9 figs.
1923. A new species of hawkmoth from Borneo. *Novit. zool.* **30** : 268, 269, 2 figs.
1923. List of the butterflies figured on Plate IV. *Novit. zool.* **30** : 270, pl. 4.
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1924. On *Hypocista* and some allied genera of Satyrinae (Lep. Rhop.) from New Guinea and the Solomon Islands. *Novit. zool.* **31** : 279–297.
1924. Two new subspecies of Sphingidae. *Novit. zool.* **31** : 298.

1925. Siphonaptera. In Th. Monod, Parasitologia Mauritanica, materiaux pour la faune parasitologique en Mauritanie. *Bull. Com. A. O. F.* **1925** : 101, 102.
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1925. Siphonaptera collected by Rear-Admiral H. Lynes in Darfur in 1920 to 1922. *Novit. zool.* **32** : 113.
1925. New Oriental Zygaenidae. *Novit. zool.* **32** : 230–237.
1925. A new species of Anthribidae from Sumatra collected by E. Jacobson. *Novit. zool.* **32** : 238.
1925. Five new Indian Anthribidae. *Novit. zool.* **32** : 239–241.
1925. Anthribidae from the eastern hemisphere. *Novit. zool.* **32** : 242–257.
1925. On *Delias belladonna* and allied species (Lep. Rhop.). *Novit. zool.* **32** : 277–287, 8 figs.
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1928. On some Lepidoptera of special interest, with remarks on morphology and nomenclature. *Novit. zool.* **34** : 132–146, pls. 1–3.
1928. On plates IV and V, representing Oriental Epiplemidae. *Novit. zool.* **34** : 147–150, pls. 4, 5.
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1928. On the *latreillei*-group of eastern Papilios. *Novit. zool.* **34** : 159–172, pls. 6, 7.
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1929. On some Oriental Sphingidae. *Novit. zool.* **35** : 85–88, 5 figs.
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1929. On fleas collected by Dr. H. M. Jettmar in Mongolia and Manchuria in 1927 and 1928. *Novit. zool.* **35** : 155–164, pls. 7–10.
1929. Two new African species of *Ctenophthalmus* (Siphonaptera). *Novit. zool.* **35** : 165–167, 4 figs.
1929. On a small collection of Siphonaptera from the Adirondacks, with a list of the species known from the state of New York. *Novit. zool.* **35** : 168–177, 4 figs.
1929. Some new Palaearctic fleas. *Novit. zool.* **35** : 178–186, 10 figs.
1929. On *Polyptychus pygarga* and some allied species (Lep., Sphingidae). *Novit. zool.* **35** : 187–191, 12 figs.

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1930. Some new butterflies and moths from eastern New Guinea. *Novit. zool.* **35** : 277–287, 6 figs.
1930. Some new Anthribidae from tropical Africa. *Novit. zool.* **35** : 244–249.
1930. Epipyropidae from the Tring Museum. *Proc. ent. Soc. Lond.* **4** : 114.
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1930. On some South African fleas. *Novit. zool.* **36** : 129–138, 7 figs.
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1931. Siphonaptera collected by Mr. F. J. Cox in France. *Novit. zool.* **36** : 225–229, 4 figs.
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1931. On some fleas collected by Monsieur Heim de Balzac in western Algeria. *Novit. zool.* **36** : 233, 234, 4 figs.
1931. On *Cypa decolor* and some allied species (Lep., Sphingidae). *Novit. zool.* **36** : 235–242, 24 figs.
1931. On the geographical variation of the pine hawk-moth, *Hyloicus pinastri*. *Novit. zool.* **36** : 243–249, 12 figs.
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1931. Anthribidae collected by F. C. Drescher on the island of Java. *Novit. zool.* **36** : 288–302, 4 figs.
1931. Two new Oriental Anthribidae. *Novit. zool.* **36** : 303, 304.
1931. Some Anthribidae from tropical Africa. *Novit. zool.* **36** : 305–310, 1 fig.
1931. Three new South American fleas. *Novit. zool.* **36** : 311–316, 5 figs.
1931. Both sexes of *Papilio aristor*, God., from San Domingo. *Proc. ent. Soc. Lond.* **6** : 62.
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1931. Further records and descriptions of fleas from Ecuador. *Novit. zool.* **37** : 135–143, 12 figs.
1931. Three new Old World fleas. *Novit. zool.* **37** : 144–147, 6 figs.

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1932. Siphonaptera collected by Mr. C. Elton in Lapland. *Novit. zool.* **38** : 258–260, 1 fig.
1932. Siphonaptera collected by Herr Georg Stein in the High Tatra. *Novit. zool.* **38** : 261–263, 4 figs.
1932. A new *Xenopsylla* from Hawaii. *Novit. zool.* **38** : 264–266, 4 figs.
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1932. Siphonaptera collected by Harold Stevens on the Kelley-Roosevelt expedition in Yunnan and Szechuan. *Novit. zool.* **38** : 276–290, 17 figs.
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1936. Two new African Syntomidae. *Novit. zool.* **39** : 293, 2 figs.
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1936. Some Siphonaptera from South America. *Novit. zool.* **39** : 305–310, 9 figs.
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RÉVISION DES ESPÈCES AFRICAINES DU GENRE *EPOMIS* BONELLI (COLEOPTERA : CARABIDAE).

Par P. Basilewsky.

(*Chef de la Section d'Entomologie du Musée Royal du Congo Belge, à Tervuren.*)

Avec 16 Texte-figures.

Cette révision des espèces africaines et malgaches du genre *Epomis* rentre dans le cadre de mes études sur la systématique des Chléniens de l'Afrique Noire. C'est avec une très vive joie que je dédie ce mémoire à l'éminent savant H. E. Karl Jordan, et je suis particulièrement heureux d'avoir été invité à collaborer au Volume Jubilaire publié en son honneur par la Royal Entomological Society of London.

Je prie mon éminent collègue de bien vouloir accepter la dédicace de ce travail en témoignage de profonde sympathie et de vive admiration et en reconnaissance pour sa longue et combien précieuse collaboration avec la Section d'Entomologie du Musée Royal du Congo Belge à Tervuren.

Le genre *Epomis* rentre dans la tribu des Chlaeniini de la sousfamille des Chlaeniinae, telle qu'elle a été définie dans mes études antérieures, par les épipleures élytraux tordus en avant de l'apex, par les protarses des mâles fortement dilatés et pourvus à la face ventrale d'une semelle entière de phanères adhésives, par le repli basilaire de l'élytre complet et par le menton profondément échancré. Il diffère des autres genres de la tribu par l'ensemble des caractères suivants : dent labiale présente et bifide ; troisième article des antennes plus long que le quatrième ; profémurs dissemblables chez les deux sexes, ceux du mâle carénés à la base de la partie ventrale ; dernier article des palpes labiaux et maxillaires fortement dilaté et longuement pubescent. Se rapprochant le plus de *Terraleus* Fairmaire, de Madagascar, il en diffère surtout par la dent labiale bifide, par la sculpture des intervalles élytraux et par la dent basale des profémurs du mâle remplacée par une crête.

L'étude des espèces de ce genre, comme d'ailleurs celle de tous les Chléniens, n'est possible qu'après l'examen des types. De nombreux auteurs ont attaché une trop grande importance à la coloration et au dessin élytral, tout en négligeant l'observation de caractères qui se sont avérés primordiaux ; il en résulte que les descriptions sont toujours insuffisantes et que l'examen de l'exemplaire ayant servi à cette description peut seul permettre avec certitude une détermination exacte. J'ai eu le privilège de pouvoir étudier l'énorme majorité des types des Chlaeniinae d'Afrique existant à l'heure actuelle et j'ai ainsi contracté une lourde dette de reconnaissance envers ceux qui ont bien voulu mettre à ma disposition les matériaux confiés à leur garde. Je remercierai ici tout particulièrement MM. E. B. Britton, du British Museum (Natural History), de Londres, L. Chopard et R. Jeannel, du Muséum National d'Histoire Naturelle de Paris, K. Delkeskamp, du Zoologisches Museum de Berlin, A. J. Hesse, du South African Museum de Cape Town, Z. Kaszab, du Musée National Hongrois de Budapest et R. Malaise, du Naturhistoriska Riksmuseum de Stockholm.

Ma gratitude va aussi à tous ceux, trop nombreux pour être cités ici, qui, par la communication de collections souvent importantes, m'ont permis d'étendre nos connaissances sur la distribution des espèces.

Abbréviations utilisées :

BM—British Museum (Nat. Hist.), London ;
MP—Muséum National d'Histoire Naturelle, Paris ;
MRCB—Musée Royal du Congo Belge, Tervuren ;
MS—Naturhistoriska Riksmuseum, Stockholm ;
SAM—South African Museum, Cape Town.

Dans une publication récente (Basilewsky et Grundmann, 1954, *Bull.* (*Ann.*) *Soc. ent. Belg.* **90** : 239–259) j'ai eu l'occasion de préciser les raisons qui m'amènent à reconnaître la paternité de Bonelli pour les genre *Callistus*, *Chlaenius*, *Dinodes* et *Epomis* ; je n'y reviendrai donc plus.

EPOMIS Bonelli.

Bonelli, 1809, *Mem. Acad. Torino* **18**, Tab. synopt. Dejean, 1826, *Spec. Col.* **2** : 368 ; 1830, *Icon. Col. Eur.* **2** : 193 ; 1831, *Spec. Col.* **5** : 593. Chenu, 1851, *Encycl. Hist. Nat., Col.* **1** : 177. Laferté, 1851, *Ann. Soc. ent. Fr.* (2) **9** : 213, 252. Lacordaire, 1854, *Gen. Col.* **1** : 223. J. du Val, 1857, *Gen. Col. Eur.* **1** : 16. Redtenbacher, 1858, *Fauna Austr.* 2. Aufl. : lx, 29 ; 1874, *id.*, 3. Aufl. : lxiii, 30. Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 16, 20. Seidlitz, 1887, *Fauna Balt.* 2. Aufl., Art. 28 ; 1888, *Fauna Transsylv.* Art. : 28. Ganglbauer, 1892, *Käf. Mitteleur.* **1** : 386. Bedel, 1897, *Cat. rais. Col. N. Afr.* **1** : 94. Csiki, 1907, *Magyar. Bogarf.* **1** : 286. Reitter, 1908, *Fauna Germ.* **1** : 184. C. Schaufuss, 1916, *Calw. Käferb.*, 6. Aufl. **1** : 53. Andrewes, 1919, *Trans. ent. Soc. Lond.* **1919** : 91. Porta, 1923, *Fauna Col. Ital.* **1** : 214. Puel, 1925, *Carab. franco-rhén.* **2** : 9, 12. Burgeon, 1935, *Bull.* (*Ann.*) *Soc. ent. Belg.* **75** : 49 ; 1935, *Ann. Mus. Congo Belge*, Sér. in-4° (Zool.) **3** : 2 (Carab.) : 233. Lutshnik, 1933, *Casopis* **30** : 169. Boldori, 1940, *Boll. Soc. ent. ital.* **12** : 165, 168. Jeannel, 1942, *Faune Fr.* **40** (Carab.) : 961, 962 ; 1949, *Faune Emp. franç.* **11** (Col. Carab. rég. malg.) : 784, 796. Basilewsky, 1950, *Bull.* (*Ann.*) *Soc. ent. Belg.* **86** : 46. Basilewsky et Grundmann, 1954, *Bull.* (*Ann.*) *Soc. ent. Belg.* **90** : 247.

Espèce-type : *circumscriptus* Duftschmidt (*Cfr.* Basilewsky & Grundmann, 1954, *loc. cit.* : 247).

Taille moyenne à grande. Dessus du corps à pilosité variable, le plus souvent limitée aux côtés et à l'apex des élytres. Coloration souvent métallique, les élytres avec ou sans bordure jaune.

Tête forte, à sculpture modérée, les yeux gros et très saillants, les tempes longues et faiblement obliques. Mandibules moyennes, larges à la base, recourbées et aiguës au sommet, à face externe faiblement ridulée. Palpes longs, à dernier article longuement pubescent, à dilatation variable chez le mâle, les labiaux polychètes. Dent labiale large, bifide au sommet. Antennes longues, dépassant la base du pronotum de 3 à 4 articles, les articles 1 à 3 à pubescence rare et longue, 4 à 11 à pubescence serrée et courte, le troisième article plus long que le suivant.

Pronotum non ou modérément transversal, à largeur maximale située au milieu de la longueur ou déportée en avant, à sculpture variable, à sillon longitudinal médian fin mais long, à repli latéral faible, à gouttière marginale étroite et peu profonde, pas élargie en arrière, le bord antérieur non rebordé, de même que le postérieur, sans sillons transversaux, à dépressions basilaires assez profondes et allongées. Ecusson en triangle large à la base. Elytres assez larges, à épaule arrondie et bien marquée, à repli basilaire complet, modérément anguleux à l'épaule, à troncature apicale oblique et non sinuée ; épipleures élytraux tordus un peu avant l'apex ; stries étroites mais profondes ; intervalles convexes ou subplans ; striole scutellaire assez longue et droite.

Apophyse prosternale en fer de lance, non rebordée, avec une touffe de soies à son extrémité. Métépisternes allongés, environ deux fois aussi longs que larges au bord antérieur, peu rétrécis en arrière, à sillon externe longitudinal faible et incomplet.

Chétotaxie : Bord antérieur du labre avec 6 soies, les deux externes éloignées des autres. Soie prothoracique latérale antérieure absente, la postérieure située dans la gouttière, assez loin en avant de l'angle postérieur. Fouet basilaire de l'élytre à l'origine de la première strie. Pores discaux de l'élytre indistincts. Série ombiliquée formée d'une vingtaine de fouets, peu distincts dans la pubescence générale. Soies abdominales présentes. Deux soies anales chez le mâle, 4 chez la femelle.

Mâle.—Trois premiers articles des protarses fortement dilatés. Profémurs avec une crête ventrale plus ou moins nette, formée par la suture intéro-antérieure formant une saillie vers la base. Palpes à dernier article ordinairement plus élargi au sommet.

Edéage volumineux, très allongé, partie basale très arquée, bulbe basal bien développé et fermé, surface dorsale membraneuse étendue sur une grande longuer du lobe médian.

Dans le *Coleopterorum Catalogus*, 1931, pars 115 : 940, Csiki attribue comme synonymes à *Epomis* les noms suivants : *Tomochilus* Laferté, *Eurydactylus* Laferté, *Aeacus* Laferté et *Dilobochilus* Laferté. Il s'agit, en réalité, de coupes groupant des espèces très différentes, n'ayant pour toute similitude qu'une plus ou moins forte dilatation des palpes.

Le genre *Epomis* est surtout répandu en Afrique, où il compte 17 espèces, dont une occupe également toute la région méditerranéenne et le Proche-Orient et dont trois sont spéciales à Madagascar. Cependant l'aire de dispersion de ce genre s'étend jusqu'au Sud-Est asiatique, car les espèces suivantes lui appartiennent également : *dejeani* Dejean (Italie, Hongrie, Grèce, Asie mineure), *amarae* Andrewes (Mésopotamie), *louwerensi* Andrewes, *duvauceli* Dejean et *nigricans* Wiedemann (Inde et Asie Sud-Est).

TABLEAU DES ESPÈCES.

1 (18) Elytres plus ou moins largement bordés de jaune.

2 (9) Intervalles des élytres lisses, avec seulement une rangée de points le long des stries.

3 (6) Pronotum non cordiforme, à largeur maximale située au milieu de la longueur, à base plus large que le bord antérieur.

4 (5) Taille plus petite. Dernier article des palpes labiaux et maxillaires à pubescence plus forte, particulièrement dilaté et sécuriforme chez le mâle qui a le bord antérieur de cet article aussi large que la moitié de sa longueur totale. Pronotum peu transverse. Elytres plus allongés et subparallèles, les intervalles convexes, pourvus d'une rangée de points alignés le long des stries, à microsculpture formant un réseau isodiamétral peu net. Proépisternes à ponctuation faible et rare. Abdomen glabre et imponctué
1. **circumscriptus** Duftschmidt

5 (4) Taille plus forte. Dernier article des palpes labiaux et maxillaires à pubescence plus faible, pas plus dilaté chez le mâle que chez la femelle, a bord antérieur bien plus étroit que la moitié de la longueur. Pronotum bien transverse. Elytres plus courts et plus trapus, les intervalles subplans, pourvus d'une ou deux rangés de points alignés le long des stries, le huitième entièrement ponctué, à microsculpture formant un réseau isodiamétral net. Pubescence du dessus plus abondante et plus longue. Proépisternes à ponctuation plus abondante. Abdomen pubescent et ponctué . . . . 2. **croesus** Fabricius

6 (3) Pronotum cordiforme, à largeur maximale fortement déportée en avant du milieu, à base plus étroite que le bord antérieur, les côtés fortement rétrécis vers l'arrière, les angles postérieurs en lobes.

7 (8) Elytres convexes sur le disque, à intervalles très convexes. Pronotum non transversal et pas particulièrement élargi en avant, bien que la largeur maximale se trouve déportée en avant du milieu, moins cordiforme. Tête à ponctuation abondante. Dernier article des palpes labiaux et maxillaires pas plus dilaté chez le mâle que chez la femelle, le bord antérieur bien plus étroit que la moitié de la longueur totale de l'article . . . . 3. **protensus** Chaudoir

8 (7) Elytres particulièrement aplanis sur le disque, à intervalles moins convexes. Pronotum très transversal, particulièrement élargi en avant ce qui lui donne un fort aspect cordiforme. Tête à ponctuation presque nulle. Dernier article des palpes labiaux et maxillaires particulièrement dilaté chez le mâle, à bord antérieur aussi large que la moitié de la longueur totale de l'article . . . . 4. **deplanatus** Laferté

9 (2) Intervalles pairs densément ponctués chagrinés, les impairs le plus souvent avec une ligne lisse au milieu, ou tous les intervalles ponctués mais avec une ligne lisse au milieu.

10 (17) Pronotum plus large que long, plus ou moins transverse.

11 (12) Sculpture du pronotum très grossière, consistant en points particulièrement gros, séparés par des parois élevées entremêlées, donnant à toute la surface un aspect couturé 5. **latreillei** Laferté

12 (11) Sculpture du pronotum consistant en points assez gros et profonds mais isolés, sans aucune paroi élevée entre eux, la surface n'étant nullement couturée.

13 (16) Surface du pronotum à ponctuation rare, les points séparés par des espaces lisses considérables.

14 (15) Côtés du pronotum peu arrondis, la base plus ou moins de la même largeur que le bord antérieur ; largeur maximale située au milieu de la longueur. Bande longitudinale médiane lisse du cinquième intervalle moins marquée . . 6. **bocandéi** Laferté

15 (14) Côtés du pronotum plus largement arrondis, la base plus large que le bord antérieur ; largeur maximale située en arrière du milieu. Bande longitudinale médiane lisse du cinquième intervalle mieux marquée . . . . 7. **rhodesianus** Péringuey

16 (13) Surface du pronotum à ponctuation très rapprochée et très dense . . . . 8. **alluaudi** Fairmaire

17 (10) Pronotum plus long que large, nullement transversal. 9. **fimbriatus** Klug

18 (1) Elytres sans bordure latérale jaune.

19 (30) Intervalles des élytres lisses ou avec une rangée de points le long des stries.

20 (29) Dessus convexe, intervalles bombés. Tête fortement épaissie en arrière des yeux.

21 (22) Avant-corps noir, les élytres d'un violet pourpré éclatant. Pronotum plus large et plus transversal. Palpes à dernier article fortement dilaté. . . . . 10. **violaceipennis** Chaudoir

22 (21) Avant-corps violet ou bleu métallique. Pronotum ordinairement plus étroit. Palpes à dernier article modérément élargi à l'extrémité.

23 (24) Pronotum large et un peu transverse . 11. **loveridgei** Basilewsky

24 (23) Pronotum pas plus large que long.

25 (28) Pronotum nettement élargi en avant, ce qui lui donne un aspect cordiforme.

26 (27) Intervalles des élytres avec de rares et faibles points alignés le long des stries . . . . 12. **immunitus** Murray

27 (26) Intervalles des élytres avec une rangée de points profonds et très nombreux de chaque côté des stries . . . . 13. **jordani** sp. n.

28 (25) Pronotum non ou à peine élargi en avant, non cordiforme. Points alignés le long des stries faibles et espacés. . 14. **elisabethanus** Burgeon

29 (20) Dessus plan, intervalles non bombés. Tête fortement rétrécie en arrière des yeux. Pronotum fortement rétréci vers l'arrière, la largeur maximale fortement déportée en avant. 15. **caffer** Boheman

30 (19) Intervalles pairs des élytres densément ponctués, ou tous les intervalles avec une ligne longitudinale lisse médiane.

31 (32) Grande taille. Elytres d'un violet bleu vif. Ponctuation de la tête et du pronotum particulièrement forte. Intervalles 3, 5 et 7 tectiformes, les autres simplement bombés, tous couverts d'une ponctuation dense, seuls ces trois avec une étroite bande lisse longitudinale médiane. Dernier article des palpes labiaux et maxillaires bien plus fortement dilaté chez le mâle, à bord antérieur aussi large que la moitié de la longueur totale de l'article . . . . 16. **lasti** Bates

32 (31) Taille moins forte. Elytres noirâtres. Ponctuation de la tête et du pronotum faible. Tous les intervalles également bombés, pourvus d'une ponctuation modérée, les cinq premiers lisses au milieu. Dernier article des palpes labiaux et maxillaires à peine plus dilaté chez le mâle que chez la femelle, le bord antérieur bien plus étroit que la moitié de la longueur totale de l'article . . . . 17. **elongatus** Klug

1. *Epomis circumscriptus* Duftschmidt.

Duftschmidt, 1812, *Fauna Austr.* **2** : 166. Dejean, 1826, *Spec. Col.* **2** : 369. Dejean et Boisduval, 1830, *Icon. Col. Eur.* : 194, pl. 96, fig. 1. Lucas, 1846, *Expl. Sci. Alg.* **2** : 42. Chenu, 1851, *Encycl. Hist. nat.* **1** : 178, fig. 334. Fairmaire et Laboulbène, 1854, *Faune ent. franç.* **1** : 57. Redtenbacher, 1858, *Fauna Austr.*, 2. Aufl. : 29 ; 1874, *id.*, 3. Aufl. : 30. Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 124. Gredler, 1877, *Verh. zool.-bot. Ges. Wien* **27** : 504. Marseul, 1880, *Abeille* **19** : 183. Putzeys, 1880, *J. sci. Math. Phys. nat. Lisboa* **29** : 37. Bedel, 1881, *Faune Col. Bass. Seine* **1** : 56 ; 1897, *Cat. rais. Col. N. Afr.* **1** : 94. Ganglbauer, 1892, *Käf. Mitteleur.* **1** : 386, 387. Kolbe, 1897, *Käf. D.O. Afrika*, 68. Csiki, 1907, *Magyar. Bogarf.* **1** : 287. Porta, 1923, *Fauna Col. Ital.* **1** : 214. Puel, 1925, *Misc. ent.* **28**, *Col. franco-rhén.*, *Carab.* **2** : 12, 16. Schatzmayr, 1936, *Publ. Mus. ent. P. Rossi* **1** : 64, 66. Alluaud, 1937, *Ann. Mag. nat. Hist.* (10) **19** : 282. Boldori, 1939, *Mem. Soc. ent. ital.* **18** : 285 (Larve) ; 1942, *Boll. Soc. ent. ital.* **74** : 116 ; 1949, *Atti Soc. ital. Sci. nat.* **88** : 11, fig. 1 (Larve). Jeannel, 1942, *Faune Fr.* **40**, *Carab.* **2** : 963. Basilewsky, 1946, *Ark. Zool.* **38** (A) (18) : 19.

cinctus Rossi, 1790, *Fauna Etrusca* **1** : 212, pl. 4, fig. 9 (*Carabus*) (nec Fabricius, 1781).

goryi Gray, 1832, *in* Griffith, *Anim. Kingd.* **14** : 276, pl. 15, fig. 5. Chaudoir, 1856, *Bull. Soc. Nat. Moscou* **16** : 423.

capensis Gory, 1833, *Ann. Soc. ent. Fr.* **2** : 228. Boheman, 1848, *Ins. Caffr.* **1** : 158 ; 1860, *Öfv. Vet. Akad. Forh.* : 11. Chaudoir, 1856, *Bull. Soc. Nat. Moscou* **29** : 237 ; 1876, *Ann. Mus. Stor. nat. Genova* **8** : 125. Péringuey, 1896, *Trans. S. Afr. phil. Soc.* **7** : 491, 514 ; 1926, *Ann. S. Afr. Mus.* **23** : 585, 593. Heyne-Taschenberg, 1908, *Exot. Käf.* : 22. Basilewsky, 1953, *Explor. Parc Nat. Upemba*, **10**, Carab. : 132 (**Syn. nov.**).

senegalensis Gory, 1833, *Ann. Soc. ent. Fr.* **2** : 229 (nec Dejean, 1831). Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 125. Alluaud, 1926, *in* Sjöstedt, *Ark. Zool.* **18** (A) (24) : 4 (**Syn. nov.**).

Karelini Mannerheim, 1843, *Bull. Soc. Nat. Moscou* **16** : 423.

brevicollis Chaudoir, 1843, *Bull. Soc. Nat. Moscou* **16** : 756 ; 1876, *Ann. Mus. Stor. nat. Genova* **8** : 124 (**Syn. nov.**).

turcmenicus Motschulsky, 1864, *Bull. Soc. Nat. Moscou* **37** : 345.

africanus Kuntzen, 1919, *Mitt. zool. Mus. Berlin* **9** : 149. Burgeon, 1935, *Bull. (Ann.) Soc. ent. Belg.* **75** : 49 ; 1935, *Rev. Zool.-Bot. afr.* **27** : 391 ; 1935, *Ann. Mus. Congo Belge*, Sér. in-4°, Zool., **3**, 2, Carab. : 233 (**Syn. nov.**).

tschitscherini Jedlicka, 1953, *Ann. hist.-nat. Mus. hung.* **3** : 113 (**Syn. nov.**).

Cette espèce fut décrite pour la première fois par Rossi en 1790, sous le nom de *Carabus cinctus*. Cette désignation ayant déja été utilisée par Fabricius en 1781, le nom de Duftschmidt fut adopté dès 1826 par Dejean. Je n'ai pas vu les types de Rossi ni de Duftschmidt qui n'existent probablement plus. L'espèce étant parfaitement connue depuis près de cent cinquante ans, cet examen ne serait d'ailleurs d'aucune utilité.

Synonymies. Bien que répandu sur une aire immense, *E. circumscriptus* ne varie guère ou, tout au moins, ses variations ne dépassent pas le stade individuel. Bien que plusieurs formes en aient été décrites de régions différentes, j'ai pu me convaincre par l'examen de très nombreux exemplaires que ces variations se rencontrent chez des individus de provenances les plus variées, n'affectant nullement des populations entières et ne présentant nulle part de caractère local. Elles ont d'ailleurs été créées sur des spécimens isolés, ce qui explique les légères différences constatées par leurs auteurs.

Karelini Mannerheim et *turcmenicus* Motschulsky ont été mis en synonymie de *circumscriptus* par Chaudoir (1876).

J'ai vu les types de *goryi* Gray, *capensis* Gory, *senegalensis* Gory et *brevicollis* Chaudoir dans la collection Oberthür, au Muséum National d'Histoire Naturelle de Paris ; il s'agit là de variantes individuelles insignifiantes. Le nom d'*africanus* fut donné par Kuntzen pour remplacer celui de *capensis* Gory, préoccupé ; il ne doit donc pas être retenu. Enfin, j'ai pu voir le type de *tschitscherini* Jedlicka, des collections du Musée de Budapest, et cet exemplaire ne diffère nullement de *circumscriptus* ; son auteur n'a pas remarqué qu'il s'agissait d'un *Epomis* et l'a comparé, dans sa description, à des espèces d'autres genres.

Long.—16–25 mm.—Tête d'un vert métallique plus ou moins foncé, parfois avec de légers reflets pourprés ; labre et mandibules d'un ferrugineux testacé ; pronotum et élytres noirâtres, le premier avec de légers reflets verdâtres, les seconds avec une large bordure jaune testacée s'étendant sur l'intervalle 9 et la gouttière latérale ; antennes, pattes et palpes testacés jaunâtres ; dessous brun de poix, plus clair au milieu du corps, légèrement irisé sur les côtés, l'abdomen avec une bordure jaune claire de largeur variable ; épipleures des élytres testacés. Pubescence rare sur l'avant-corps, un peu plus dense sur les élytres où elle est surtout concentrée latéralement et en arrière.

Tête à ponctuation rare et modérément grosse ; bord antérieur du labre légèrement échancré. *Pronotum* un peu plus large que long, mais non ou très modérément transversal ; largeur maximale située au milieu de la longueur ou très faiblement déportée en avant ; bord antérieur droit ; côtés arrondis en avant, sub-rectilignes vers les angles postérieurs, qui sont très largement arrondis et obliques ; base plus large que le bord antérieur ; dépressions basilaires allongées, profondes et assez larges ; surface couverte de gros points, très espacés et irrégulièrement disposés. *Elytres* allongés, subparallèles, modérément convexes ;

stries fines et profondes, à crénulation peu distincte ; intervalles convexes, avec de chaque côté une file de points assez gros et espacés, disposés le long des stries ; microsculpture formant un réseau isodiamétral peu net.

Proépisternes à ponctuation rare, absente sur les côtés ; métépisternes à ponctuation plus dense ; abdomen imponctué au milieu, chagriné latéralement ; dessous glabre. *Edéage :* fig. 1.

La larve de cette espèce a été décrite par L. Boldori.

E. circumscriptus a une aire de répartition extrêmement vaste, s'étendant des Canaries à l'Iran et de l'Europe méridionale jusqu'au Cap. L'espèce fut décrite d'Autriche, mais cette indication s'avéra erronée. Très fréquente dans toute la zone méditerranéenne, elle remonte en France jusqu'à Paris, existe dans tout le Proche Orient jusqu'en Iran, et est très fréquente dans tout le Nord de l'Afrique. En Afrique Noire elle est répandue partout, mais surtout en région de savanes, bien plus rare en Afrique Occidentale et Centrale que dans la partie orientale et méridionale du Continent :

SÉNÉGAL : Saint Louis (MP). GAMBIE : MacCarthy Island (*Svensson;* MS). HAUTE-VOLTA : Pundu (*Olsufiew*; MS; MRCB).

NUBIE (sec. *Kolbe*). ETHIOPIE : Adda Shores of Hora Harsadi, xii.1926 (*J. Omer-Cooper ;* BM). ERYTHRÉE : Ghinda (MRCB, Mus. Vienne), Cheren (MP, coll. Grundmann, coll. Klynstra), Asmara (*De Lotto*, coll. Straneo). SOUDAN : Gondokoro (sec. *Gredler*). KENYA : Kibwezi, xii.1903 (*Ch. Alluaud ;* MP), Narossera, Loita plains, ii.1913 (*G. Babault ;* MP), Nairobi, ii.1924 (*van Someren ;* MP, MRCB), Morogoro, xi.1916 (*A. Loveridge ;* Mus. Comp. Zool.). TANGANYIKA TERRITORY : Dar-es-Salaam (Mus. Vienne), Zanzibar (MP) UGANDA : Lac Victoria-Nyanza, I. Ukerewe, x.1937 (*R. P. Conrads ;* MRCB).

GABON : Lambaréné, 1896 (*E. Haug ;* MP), N'Gomo, Bas Ogooué, 1906 (*id.*, MP).

CONGO BELGE : Région de Sassa 1895–96, (*Colmant ;* MRCB), Kunungu, 1938 (*N'Kele ;* MRCB), Kapanga, i.1933 (*F. G. Overlaet ;* MRCB), Sandoa, xii.1931, i.1932, vi.1933 ((*id.*) ; MRCB), Mabwe, viii.1947 (*Miss. G. F. de Witte ;* Inst. Parcs Nat. Congo Belge).

S. ANGOLA : Mungobi, 50 mls. W. Namakunda (*C. Koch ;* MRCB), Namakunda (*id. ;* MRCB, coll. Nègre), Omupanda (*id. ;* MRCB). SUD-OUEST AFRICAIN : Gross-Okatjeru, 50 km. S. Waterberg (sec. *Kuntzen*), Umg. Windhuk (*Henrichsen*, Deutsch. Ent. Inst.), Oshikango, vi.1937 (*V. Fitzsimmons ;* Transv. Museum), Kaokoveld, Kowares, 90 mls. S.E. Ohopoho, vi.1951 (*P. Brinck & Rudebeck ;* Mus. Lund). BECHUANALAND : Lac N'Gami (sec. *Boheman*), Enkoken (sec. *Péringuey*). N.W. RHODESIA : Namwala (*H. Dolman ;* BM). S. RHODESIA : Salisbury (*G. A. K. Marshall ;* BM ; MRCB). MOZAMBIQUE : Beira, vii.1903, xii.1905 (*P. Sheppard ;* BM, SAM), Rikatla (sec. *Péringuey*). TRANSVAAL : Pretoria (sec. *Péringuey*), Lydenburg (sec. *Péringuey*), Merico (Mus. Vienne), Noordhoel (coll. Klynstra). NATAL : Van Reenen, Drakensberg, xi.1926 (*R. E. Turner ;* BM), Durban, iii.1904 (*Bell Marley ;* BM), Malvern (Durban Mus.). CAPE PROVINCE : Cape Town (MRCB, BM, MP, Univ. Pretoria), Dunbrody, 1905 (*J. O'Neil ;* SAM ; MP), Grahamstown (sec. *Péringuey*), Stellenbosch (*id.*), Paarl (*id.*), Port Elizabeth (*id.*), Willowmore (*id.*), Milnerton, ii.1926 (*R. E. Turner ;* BM), Worcester (MRCB, Univ. Pretoria), Uitenhage (Durban Museum).

2. *Epomis croesus* Fabricius.

Fabricius, 1801, *Syst. El.* **1** : 183 (*Carabus*). Dejean, 1831, *Spec. Col.* **5** : 667. Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 124. Fairmaire, 1891, *Ann. Soc. ent. Belg.* **25** : ccclxxx. Kolbe, 1897, *Käfer D. O. Afrika* : 68. Heyne-Taschenberg, 1908, *Exot. Käfer* : 22. Alluaud, 1922, *Voy. Rothschild Ethiopie, Ins. Col.* : 496 ; 1939, *Miss. Sci. Omo* **5** : 19. Basilewsky, 1946, *Ark. Zool.* **38** (A) (18) : 19 ; 1950, *Mém. Inst. franç. Afr. noire* **10** : 248 ; 1953, *Bull. Inst. franç. Afr. noire* **15** : 1035.

Long. 25–30 mm.—Tête et pronotum d'un vert métallique, la première plus claire ; labre et mandibules ferrugineuses ; élytres noirâtres, avec de légers reflets verdâtres surtout sur les côtés et à la base, largement bordés latéralement de jaune testacé, cette bordure s'étendant sur l'intervalle 9 et la gouttière marginale ; palpes, pattes et antennes d'un ferrugineux clair, tarses et articles 4 à 11 des antennes plus foncés ; dessous brun de poix très foncé, sans aucune irisation latérale ; épipleures testacés ; abdomen à bordure jaune latérale très étroite. Pubescence du dessus jaune, assez abondante et longue, surtout sur les côtés et en arrière des élytres.

Tête particulièrement grosse, très convexe et large en arrière des yeux, à ponctuation rare et modérée ; échancrure du bord antérieur du labre très faible. Dernier article des palpes labiaux et maxillaires modérément pubescent, pas plus dilaté chez le mâle que chez la femelle, à bord antérieur bien plus étroit que la moitié de la longueur totale de l'article.

Pronotum nettement transversal, plus large que long, à largeur maximale située au milieu de la longueur ; bord antérieur subdroit, les angles antérieurs bien marqués ; côtés arrondis sur toute leur longueur, plus rétrécis vers l'avant ; angles postérieurs largement arrondis mais bien moins obliques que chez *circumscriptus* ; ponctuation de la surface assez grosse, plus dense que chez cette dernière espèce mais assez peu serrée quand même ; dépressions basilaires moins profondes et moins allongées que chez *circumscriptus*. *Elytres* particulièrement larges et trapus ; stries fines mais assez peu profondes, faiblement crénelées ; intervalles subplans, pourvus d'une ou deux rangées de faibles points alignés le long des stries, le huitième entièrement ponctué ; microsculpture formant un réseau isodiamétral dense et bien net.

Proépisternes à ponctuation assez grosse, éparse mais étendue sur toute la surface ; métépisternes à ponctuation plus dense ; tout le dessous légèrement ponctué et pubescent. Crête ventrale du profémur mâle moins nette que chez l'espèce précédente. *Edéage :* fig. 2.

Je n'ai pas vu le type de Fabricius et je ne sais s'il existe encore ; mais l'espèce est parfaitement connue et cet examen n'est guère nécessaire.

E. croesus a une répartition géographique très caractéristique, d'un type sahélien très net ; il est surtout fréquent en Mauritanie mais devient rare vers l'Est.

MAURITANIE : Trarza (MRCB, IRSNB), Boghé (MRCB), région de Guidimaka, 1908 (*G. Cuidan ;* MP), Kaedi (MP). SÉNÉGAL : Saint Louis, 1894 (*Lallier ;* MP), env. Saint Louis, vii.1952 (*Dr. L. Laurent ;* MRCB), Rufisque (*G. Favarel ;* MRCB), Nioro, 1918 (*R. Chudeau ;* MP). GAMBIE : MacCarthy Island (*Svensson ;* MS, MRCB). GUINÉE PORTUGAISE : Ile de Bissao (*G. Favarel ;* MP). SOUDAN : Siguiri (MP), Toara, xi.1949 (*Daget & Mougin ;* IFAN, MRCB). HAUTE VOLTA : Pundu (*Olsufiew ;* MS, MRCB). NIGER : Aïr, Mts. Tarraouji, ix.1947 (*L. Chopard & A. Villiers ;* IFAN, MRCB). N. NIGERIA : Sherifuri, near Azare, 1926 (*Dr. Ll. Lloyd ;* BM). TCHAD : N'Guigmi, 1919 (*Dr. Noel ;* MP), Fort Lamy, 1904 (*J. Decorse ;* MP), de Fort Lamy à Mandjaffa (*id. ;* MP).

NUBIE (sec. *Chaudoir*). SOMALI (sec. *Fairmaire*). S. ETHIOPIE : Nanoropus, sur le lac Rodolphe, i.1933 (*Miss. Omo ;* MP). KENYA : Mts. Matthews, riv. Gourani, 1905 (*M. de Rothschild ;* MP).

3. *Epomis protensus* Chaudoir.

Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 125. Burgeon, 1935, *Bull.* (*Ann.*) *Soc. ent. Belg.* **75** : 49 ; 1935, *Ann. Mus. Congo Belge*, Ser. in 4°, (*Zool.*) **3**, 2, Carab. : 233.

Long. 20–24,5 mm.—Avant-corps d'un vert plus vif sur la tête que sur le pronotum ; labre et mandibules d'un brun ferrugineux ; élytres noirâtres, largement bordés latéralement de jaune, cette bordure s'étendant sur les intervalles 8 et 9 et la gouttière marginale, nettement élargie à l'apex ; dessous brun de poix foncé, plus clair au milieu ; épipleures élytraux testacés ; abdomen étroitement bordé de jaune ; pattes, palpes et antennes d'un jaune testacé. Pilosité du dessus rare et courte.

Tête large et courte, épaisse en arrière des yeux, à ponctuation rare et irrégulière ; bord antérieur du labre droit ; dernier article des palpes labiaux et maxillaires semblable chez les deux sexes, à peine élargi à l'extrémité.

Pronotum plus large que long mais modérément transversal, à largeur maximale située en avant du milieu ; bord antérieur droit, les angles antérieurs bien marqués ; côtés en courbe régulièrement arrondie en avant mais prolongée en ligne droite et rétrécie jusqu'aux angles postérieurs qui sont largement arrondis et un peu en forme de lobes vers l'arrière ;

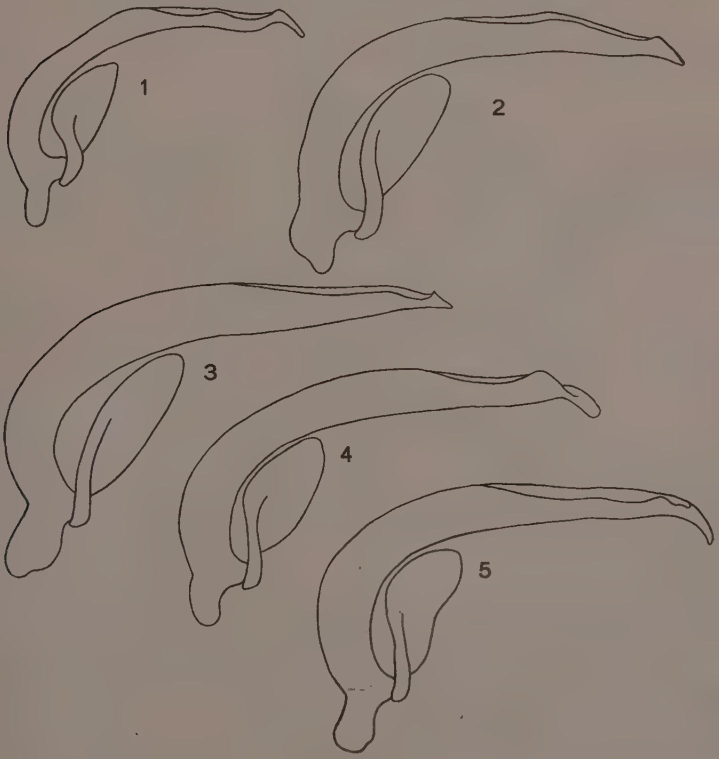

Fig. 1 à 5.—Edéages. (1) *Epomis circumscriptus* Duftschmidt (Algérie). (2) *E. croesus* F. (Trarza). (3) *E. protensus* Chaudoir (MacCarthy Island). (4) *E. deplanatus* Laferté (Sénégal). (5) *E. bocandéi* Laferté (Sénégal). × 10.

base plus étroite que le bord antérieur et un peu concave ; dépressions basilaires très profondes et allongées, avec un trait linéaire dans le fond ; surface pourvue de points assez profonds et rares, très espacés. *Elytres* allongés, subparallèles, assez convexes ; stries profondes et assez fortement crénelées ; intervalles bombés, pourvus d'une ligne de points assez gros et assez espacés, alignés le long des stries, le huitième avec toute la partie externe ponctuée ; microsculpture isodiamétrale particulièrement fine et dense, visible seulement à un très fort grossissement, ce qui rend tout l'élytre brillant.

Proépisternes à ponctuation très peu profonde et rare ; métépisternes à ponctuation plus dense et régulièrement répartie ; abdomen lisse et glabre au milieu, ponctué et chagriné latéralement. *Edéage :* fig. 3.

J'ai vu le type de cette espèce, provenant de Nubie, dans la collection Oberthür, au Muséum National d'Histoire Naturelle de Paris.

E. protensus protensus est répandu dans la région sénégalo-soudanaise, loin des côtes :

SÉNÉGAL, 1869 (*Steindachner ;* Mus. Vienne). GAMBIE : MacCarthy Island (*Svensson ;* MS, MRCB). HAUTE VOLTA : Pundu (*Olsufiew ;* MS, MRCB). SOUDAN FRANCAIS : Khayes, 1899 (*G. Massiou ;* MP). N. NIGERIA : Azare, S.E. Kano, 1925, 1928–29 (*Dr. Ll. Lloyd ;* BM, MRCB).

NUBIE (*Felder*, sec. *Chaudoir*). SOUDAN ANGLO-ÉGYPTIEN : Sennaar, 1906 (*Ch. Alluaud ;* MRCB), Tonga, W. Nil (Mus. Munich).

E. protensus **promissus** subsp. n.

Diffère de la race nominale par le pronotum plus allongé et nullement transversal, bien que de même forme, c'est à dire à largeur maximale fortement déportée en avant du milieu et à base plus large que le bord antérieur, et par la coloration : pronotum noirâtre, à reflets d'un bleu violacé, tête et élytres d'un bleu violet assez foncé, ces derniers avec la même bordure jaune. *Edéage :* semblable.

Holotype : ♂ N.E. RHODESIA : Abercorn (MRCB).

Paratype : ♀ S. RHODESIA : Gatooma (MRCB).

J'ai également vu un troisième exemplaire de cette race, il y a quelques années, parmi les collections du British Museum et je l'ai déterminé alors sous le nom de *E. protensus*.

4. *Epomis deplanatus* Laferté.

Laferté, 1851, *Ann. Soc. ent. Fr.* (2) **9** : 252. Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 125.

J'ai vu le type de cette espèce dans la collection Oberthür, au Muséum National d'Histoire Naturelle de Paris ; cet exemplaire a les élytres franchement violets.

Long. 22–26 mm.—Dessus d'un bleu métallique vif, moyennement foncé, parfois avec des reflets verdâtres, parfois les élytres violacés ; ces derniers bordés latéralement de jaune testacé, cette bordure occupant le neuvième intervalle et la gouttière, à peine élargie à l'apex ; labre brun ferrugineux ; mandibules très foncées ; dessous d'un brun de poix foncé, plus clair au milieu ; épipleures des élytres ferrugineux, l'abdomen avec une bordure latérale large, d'un jaune ferrugineux ; palpes, antennes et pattes d'un ferrugineux rougeâtre. Pilosité du dessus courte et rare, d'un jaune ferrugineux.

Tête large et courte, assez épaisse en arrière des yeux, à ponctuation presque nulle ; bord antérieur du labre profondément échancré ; dernier article des palpes labiaux et maxillaires fortement dilaté chez le mâle, à bord antérieur aussi large que la moitié de la longueur totale de l'article.

Pronotum transverse à très transverse, très cordiforme par suite de l'élargissement très particulier de la partie antérieure du pronotum dont la largeur maximale est très fortement déportée en avant du milieu ; angles antérieurs largement arrondis et peu marqués ; côtés fortement arrondis, ensuite fortement rétrécis et rectilignes jusqu'aux angles postérieurs, qui forment de larges lobes ; base un peu concave, bien plus étroite que le bord antérieur ; surface convexe ; dépressions basilaires peu profondes et nullement linéaires ; surface à ponctuation rare, faible et espacée. *Elytres* particulièrement aplanis sur le disque et nullement convexes; alongés, modérément subparallèles ; stries fines, à crénulation petite mais très distincte ; intervalles un peu bombés, avec de chaque côté des points moyennement gros et très espacés, alignés le long des stries, le huitième densément ponctué sur la partie externe ; microsculpture distincte seulement à très fort grossissement, ce qui rend tout l'élytre très brillant.

Proépisternes à ponctuation faible, espacée et irrégulière ; métépisternes densément et fortement ponctués ; abdomen ponctué-chagriné et pubescent seulement latéralement. *Edéage :* fig. 4.

Espèce à répartition sahélienne, comme les deux précédentes, mais très rare dans les collections.

SÉNÉGAL : 1869 (MP, MRCB ; *Steindachner ;* Mus. Vienne).

KENYA : Tsavo River, v.1913 (*Dr. Bayer ;* MRCB).

5. *Epomis latreillei* Laferté.

Laferté, 1852, *Rev. Mag. Zool.* (2) **4** : 66. Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 121. Basilewsky, 1952, *Mém. Inst. franç. Afr. noire* **19** : 93.

Long. 23–25,5 mm.—Dessus noir, avec des reflets métalliques à peine distincts ; labre ferrugineux ; mandibules d'un brun foncé ; élytres bordés latéralement de jaune, cette bordure s'étendant sur l'intervalle 9 et la gouttière, non élargie à l'apex ; épipleures jaunes ; dessous noir de poix, le milieu un peu éclairci, les côtés très faiblement irisés, l'abdomen largement bordé de jaune ; antennes, palpes et pattes d'un ferrugineux testacé, les tarses plus foncés. Pilosité du dessus dense mais courte, couchée.

Tête large et courte, très épaisse en arrière ; ponctuation très forte et très rapprochée, surtout sur le vertex ; bord antérieur du labre droit ; dernier article des palpes labiaux et maxillaires dilatés vers le sommet, un peu plus chez le mâle que chez la femelle, mais le bord antérieur toujours moins large que la moitié de la longueur totale de l'article.

Pronotum très transversal, bien plus large que long ; bord antérieur droit, les angles antérieurs bien marqués ; côtés régulièrement arrondis sur toute leur longueur, mais plus atténués vers l'avant ; angles postérieurs largement arrondis ; base plus large que le bord antérieur, les côtés avancés en oblique ; largeur maximale située au milieu de la longueur ; dépressions basilaires subarrondies et assez profondes, bien que peu nettement délimitées ; toute la surface couverte de points gros et profonds, rapprochés, séparés par un lacis de parois surélevées et entremêlées, donnant à tout l'ensemble un aspect particulièrement couturé. *Elytres* larges et ovoïdes, plus larges en arrière qu'en avant, assez convexes ; stries fines mais profondes, distinctement mais finement ponctuées ; intervalles légèrement bombés, 1, 3, 4, 5 et 7 un peu plus hauts que les autres, mais 2, 3, 4, 5 et 7 lisses au milieu, ce qui donne des fines bandes longitudinales luisantes ; l'espace entre les points est pourvu d'une microsculpture isodiamétrale dense et serrée.

Proépisternes à ponctuation grosse et assez dense, mais plus rare vers l'extérieur ; métépisternes à ponctuation dense ; abdomen glabre et lisse au milieu.

J'ai vu le type de cette espèce dans la collection Oberthür, au Muséum National d'Histoire Naturelle de Paris.

E. latreillei est particulièrement rare, et je n'en connais que quelques exemplaires, presque tous à localisation imprécise.

Sénégal (sec. *Chaudoir*), Sedhiou (MP). Guinée Portugaise (sec. *Laferté*). Guinée Française : Kéoulenta (*M. Lamotte ;* IFAN). Côte d'Ivoire : Dimbokro (MRCB). Haut Oubangui (*Glozel ;* MP).

6. *Epomis bocandéi* Laferté.

Laferté, 1852, *Rev. Mag. Zool.* (2) **4** : 65. Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 119.

Long. 22–26 mm.—Dessus d'un vert foncé, peu métallique, les élytres plus noirâtres, la *tête* plus claire ; labre ferrugineux testacé ; mandibules brun-noires ; *élytres* avec une bordure latérale jaune sur l'intervalle 9 et la gouttière, élargie à l'apex ; dessous noir de poix, éclairci au milieu, un peu irisé sur les côtés, l'abdomen avec une large bordure testacée ; épipleures jaunes ; palpes, pattes et antennes d'un testacé clair, les tarses plus foncés. Pilosité du dessus dense, mais fine et courte, couchée. *Edéage :* fig. 5.

J'ai cru longtemps qu'il s'agissait d'une simple variante individuelle du précédent ; l'examen des types mâle et femelle de Laferté, conservés dans la collection Oberthür au Muséum National d'Histoire Naturelle de Paris, m'a convaincu de la validité spécifique de ces deux formes. Bien que très voisin de *latreillei*, *Epomis bocandéi* en diffère par les caractères suivants : coloration du dessus plus verte, la bordure jaune élytrale élargie à l'apex ; vertex bien moins ponctué ; pronotum un peu moin large, à côtés moins arrondis, à sculpture très différente, nullement couturée mais toute la surface couverte de points gros et profonds, espacés, un peu plus rapprochés seulement à la base où ils se touchent parfois ; intervalles 1 à 5 moins nettement tectiformes à l'apex, les lignes médianes lisses moins apparentes. Pour le restant ces deux espèces sont très semblables.

E. bocandéi est aussi rare que l'espèce précédente, et je n'en connais que quatre exemplaires.

Sénégal : (MRCB), Sedhiou (MP). Guinée Portugaise : (MP).
Nubie : (*Felder ;* MP).

7. *Epomis rhodesianus* Péringuey.

Péringuey, 1898, *Trans. S. Afr. phil. Soc.* **10** : 355. Burgeon, 1935, *Bull. (Ann.) Soc. ent. Belg.* **75** : 49 ; 1935, *Ann. Mus. Congo Belge*, sér. in-4°, Zool. **3**, **2**, Carab. : 234.

Long. 21–25 mm.—Coloration identique à celle de *latreillei*, dont l'espèce diffère au premier coup d'oeil par la sculpture du pronotum, qui se rapproche de celle de *bocandéi*, les points étant encore plus espacés.

Se rapproche le plus de *E. bocandéi*, mais en diffère par la coloration et surtout par la forme du pronotum. Alors que chez *bocandéi* la largeur maximale de ce dernier est située au milieu, ses côtés sont peu arrondis, pas plus rétrécis en avant qu'en arrière et sa base de même largeur que le bord antérieur, chez *rhodesianus* cette largeur maximale est située en arrière du milieu, les côtés sont plus fortement arrondis et plus rétrécis vers l'avant que vers l'arrière, et la base est de même largeur que le bord antérieur ; il est également plus largement transversal chez *rhodesianus* et la sculpture de la tête en arrière des yeux est plus forte. Les intervalles des élytres, enfin, sont un peu plus tectiformes chez *rhodesianus*, 3 et 5 à bande médiane lisse mieux marquée. *Edéage :* fig. 6.

Type au South African Museum, Cape Town (!).

Southern Rhodesia : Salisbury (SAM). Congo Belge : Kapanga, i.1931 (*F. G. Overlaet ;* MRCB), Luashi, iii.1936 (*F. Freyne ;* MRCB), Kando, iii.1931 (*G. F. de Witte ;* MRCB), Elisabethville, 1949, à la lumière (*N. Leleup ;* MRCB ; xii.1949, à la lumière, (*Ch. Seydel ;* MRCB).

8. *Epomis alluaudi* Fairmaire.

Fairmaire, 1901, *Rev. Ent.* **20** : 109. Alluaud, 1915, *Bull. Soc. ent. Fr.* : 205. Jeannel, 1949, *Faune Emp. franç.* **11**, *Col. Carab. rég. malg.* : 798, fig. 382, 383.
fimbriatus Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 122, nec Klug 1833.

Long. 23–25 mm.—Dessus noir, la tête et les côtés du pronotum avec de faibles reflets verdâtres ; labre ferrugineux, mandibules brunes foncées ; élytres bordés latéralement de jaune, cette bordure occupant le neuvième intervalle et la gouttière, faiblement élargie à l'apex ; épipleures des élytres jaunes. Dessous brun de poix très foncé, un peu plus clair au milieu, faiblement irisé latéralement, l'abdomen assez largement bordé de jaune ; palpes, antennes et pattes d'un jaune testacé, les tarses plus foncés. Pilosité du dessus très courte, très dense, dressée, fauve.

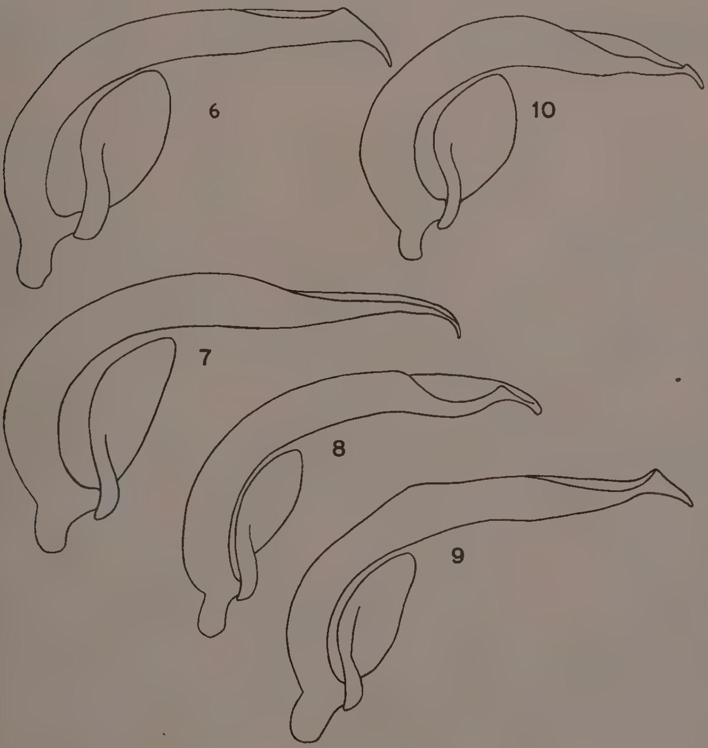

Fig. 6 à 10.—Edéages. (6) *Epomis rhodesianus* Péringuey (Elisabethville). (7) *E. alluaudi* Fairmaire (Diégo-Suarez). (8) *E. fimbriatus* Klug (Maroantsetra). (9) *E. violaceipennis* Chaudoir (Mungo). (10) *E. loveridgei* Basilewsky (Uluguru Mts.). × 10.

Tête large et courte, très épaisse en arrière ; ponctuation assez forte et dense, avec une place lisse au milieu du front ; bord antérieur du labre échancré ; dernier article des palpes labiaux et maxillaires élargi à l'extrémité, un peu plus large chez le mâle que chez la femelle, mais le bord antérieur plus étroit que la moitié de la longueur totale de l'article.

Pronotum plus large que long, un peu transverse, à largeur maximale située au milieu de la longueur ; bord antérieur droit, angles antérieurs arrondis et peu marqués ; côtés légèrement arrondis en avant, puis vers l'arrière et continués d'une manière presque rectiligne jusqu'aux angles postérieurs qui sont largement arrondis et situés au niveau de la base ; celle-ci droite et plus large que le bord antérieur ; dépressions basilaires allongées et modérément profondes ; surface couverte d'une ponctuation forte et régulière et particulièrement dense. *Elytres* oblongs et amples, modérément convexes ; stries profondes mais étroites, modérément ponctuées ; intervalles saillants, 1 à 5 et 7 un peu tectiformes sur le disque, présentant au milieu de la largeur une ligne longitudinale lisse, tandis que le restant est couvert d'une ponctuation dense.

Proépisternes à ponctuation grossière et assez rapprochée, mais laissant le côté externe imponctué ; métépisternes à ponctuation dense ; abdomen ponctué seulement latéralement, à pubescence régulière et dense, assez courte. *Edéage :* fig. 7.

Type au Muséum National d'Histoire Naturelle de Paris (!).

MADAGASCAR : Diégo-Suarez (*Ch. Alluaud ;* MP), Majunga (*Dr. J. Decorse ;* MP), Andampikely, près de Mandritsara (*Ch. Lamberton ;* MP), Fianarantsoa (*Grandidier ;* MP), Maroantsetra (MRCB), Analalava (MRCB), Vohémar (*Dr. A. Sicard ;* MP).

9. *Epomis fimbriatus* Klug.

Klug, 1833, *Abh. Akad. Wiss. Berlin* : 129. Fairmaire, 1901, *Rev. Ent.* **20** : 109. Jeannel, 1949, *Faune Emp. franç.* **11**; *Col. Carab. rég. malg.* : 798, 799.

Long. 18–21 mm.—Dessus noirâtre, la tête et les côtés du pronotum avec de forts reflets verts métalliques, les élytres très légèrement bleutés et pourvus d'une bordure latérale jaune sur le neuvième intervalle et la gouttière marginale, faiblement élargie à l'apex ; labre ferrugineux ; mandibules brunes. Dessous brun de poix, à peine irisé latéralement, épipleures testacés, abdomen avec une étroite bordure jaune ; antennes, palpes et pattes d'un jaune testacé. Pilosité du dessus fauve, dense mais peu longue.

Tête assez allongée, modérément épaissie en arrière, à ponctuation très faible ; bord antérieur du labre faiblement échancré ; dernier article des palpes labiaux et maxillaires allongé et un peu élargi à l'extrémité, plus fortement chez le mâle que chez la femelle, mais le bord antérieur toujours plus étroit que la moitié de la longueur totale de l'article.

Pronotum un peu plus long que large, à largeur maximale très faiblement déportée en avant du milieu ; bord antérieur droit, les angles antérieurs peu arrondis et bien marqués ; côtés faiblement arqués en avant et en arrière où ils sont prolongés par une ligne faiblement sinuée ; angles postérieurs largement arrondis, nullement avancés par rapport au milieu de la base ; cette dernière subdroite, de même largeur environ que le bord antérieur ; dépressions basilaires assez profondes et allongées ; surface pourvue de gros points espacés et irrégulièrement disposés, laissant de très considérables espaces lisses. *Elytres* allongés et un peu élargis en arrière, modérément convexes ; stries profondes et moins étroites que chez *alluaudi*, finement crénelées ; intervalles modérément convexes, non tectiformes, couverts d'une ponctuation assez dense, laissant une ligne médiane longitudinale lisse sur les intervalles 1 à 5 et 7.

Proépisternes à ponctuation rare et espacée, les métépisternes plus densément mais peu profondément ponctués ; abdomen à ponctuation limitée aux côtés, faiblement pubescent. *Edéage :* fig. 8.

MADAGASCAR : Maroantsetra (MP, MRCB), sud de la baie d'Antongil (MP).

10. *Epomis violaceipennis* Chaudoir.

Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 128. Burgeon, 1935, *Bull.* (*Ann.*) *Soc. ent. Belg.* **75** : 49 ; 1935, *Ann. Mus. Congo Belge*, sér. in-4°, Zool. **3**, 2, *Carab.* : 234.

Long. 19–23 mm.—Tête, pronotum et écusson d'un noir brillant, sans aucun reflet métallique ; élytres d'un violet pourpré éclatant, parfois noirâtre ou bleuté sur le disque ; dessous noir de poix, très faiblement irisé sur les côtés ; labre ferrugineux ; mandibules d'un brun noirâtre ; palpes, antennes et pattes ferrugineux rougeâtres très clairs. Pilosité du dessus très fine et courte, limitée aux côtés et à l'apex.

Tête courte et large, très épaissie en arrière des yeux, à ponctuation assez forte et régulière, le milieu du front lisse ; bord antérieur du labre subdroit ; palpes labiaux et maxillaires à dernier article fortement élargi, surtout chez le mâle le bord antérieur étant à peu près de la même largeur que la longueur totale de l'article.

Pronotum plus large que long, nettement bien que faiblement transversal ; largeur maximale située en avant du milieu ; bord antérieur droit, les angles antérieurs peu marqués ; côtés faiblement arqués en avant, légèrement sinués en arrière, angles postérieurs largement arrondis ; base à peu près de même largeur que le bord antérieur, un peu oblique sur les côtés ; dépressions basilaires profondes et allongées, un peu obliques, à fond linéaire ; surface pourvue de points gros et nombreux, bien qu'espacés et irrégulièrement disposés. *Elytres* ovoïdes, élargis plus fortement en arrière, surtout chez la femelle, assez convexes ; stries profondes et assez étroites, à ponctuation faible ; intervalles convexes et imponctués, sauf une rangée de petits points peu profonds de chaque côté des stries, le huitième fortement ponctué, surtout du côté externe.

Proépisternes à ponctuation irrégulière et absente au côté externe ; métépisternes à ponctuation plus dense mais peu profonde ; abdomen ponctué seulement latéralement, à pubescence fine et courte, limitée aux côtés. *Edéage :* fig. 9.

Le type de *E. violaceipennis*, que j'ai pu voir parmi les collections du Zoologisches Museum der Humboldt-Universität, de Berlin, provient de Cap Palmas, à la frontière du Liberia et de la Côte d'Ivoire. Cette espèce est assez largement répandue dans la zone forestière guinéenne, jusqu'au Katanga, mais n'est jamais fréquente.

NIGERIA : Lagos (MP). GOLD COAST (*Castle ;* MP). TOGO : Bismarckburg, iv.1893 (*L. Conradt ;* Mus. Berlin). CAMEROUN : Mungo, Mukonje Farm (MRCB, MP), Aborando (MP), Dibongo (MP).

CONGO BELGE : Mayumbe (*de Briey ;* MRCB), Kiobo, bassin de la Luki (*C. Donis ;* Inst. roy. Sci. nat. Belgique), Eala, vii.1933 (*A. Corbisier ;* MRCB), Kafakumba, i.1931, vi.1931, x–xi.1931, iv.1933, i.1934, iv.1934 (*F. G. Overlaet ;* MRCB), Kapanga, ii.1933 (*F. G. Overlaet ;* MRCB).

11. *Epomis loveridgei* Basilewsky.

Basilewsky, 1951, *Psyche, Camb., Mass.* **58** : 43, fig. 1.

Long. 18,5 mm.—Dessus d'un violet foncé, très brillant, l'écusson noir ; dessous noir de poix, sans aucun reflet métallique ; pattes ferrugineuses, les fémurs très foncés, presque noirs ; antennes brunes.

Tête large et courte ; surface lisse au milieu du front, avec une ponctuation légèrement espacée en arrière et sur les côtés ; bord antérieur du labre droit ; dernier article des palpes élargi chez le mâle, surtout aux labiaux.

Pronotum large, un peu transverse, faiblement convexe, un peu cordiforme ; largeur maximale déportée légèrement en avant du milieu ; angles antérieurs arrondis ; côtés modérément arqués dans le premier tiers, ensuite rétrécis et légèrement sinués ; angles postérieurs droits et arrondis ; base droite, environ de même largeur que le bord antérieur ; dépressions basilaires profondes et allongées, presque linéaires ; surface à ponctuation irrégulière et espacée, assez grosse. *Elytres* subovoïdes, faiblement convexes, à largeur maximale située à mi-longueur ; stries fines et profondes, à ponctuation distincte ; intervalles très convexes, très luisants, à microsculpture très réduite, ponctués seulement le long des stries, le huitüme à ponctuation espacée.

Dessous à pubescence presque nulle ; *proépisternes* à ponctuation grosse et espacée, limitée à la partie interne ; métépisternes densément ponctués ; abdomen ponctué-chagriné latéralement. *Edéage :* fig. 10.

Le type (♂), seul exemplaire connu, se trouve au Museum of Comparative Zoology, Harvard College, à Cambridge (U.S.A.) et provient du TANGANYIKA TERRITORY : Uluguru Mountains, Bagil, ix. 1926 (*A. Loveridge*).

12. *Epomis immunitus* Murray.

Murray, 1858, *Ann. Mag. nat. Hist.* (3) **1** : 13. Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 111.

Long. 16,5 mm.—Dessus d'un bleu violacé brillant ; labre et mandibules ferrugineux ; dessous noir de poix, un peu plus clair ; antennes, palpes et pattes testacés. Pilosité du dessus presque nulle.

Tête large, à ponctuation rare et espacée sur les côtés et en avant ; bord antérieur du labre à peine échancré ; dernier article des palpes assez fortement dilaté, presque sécuriforme.

Pronotum à peu près aussi large que long, fortement élargi en avant où se trouve la largeur maximale ; angles antérieurs peu marqués ; côtés brièvement élargis en avant, ensuite rétrécis et subsinués jusqu'aux angles postérieurs qui sont modérément arrondis et subdroits ; base un peu moins large que le bord antérieur ; dépressions basilaires profondes et allongées, obliques ; surface à ponctuation assez grosse mais particulièrement espacée, surtout concentrée près du sillon longitudinal médian. *Elytres* allongés et peu convexes, à largeur maximale située à peu près à mi-longueur ; stries profondes et finement, bien distinctement ponctuées ; intervalles plans, imponctués et très brillants, à microsculpture à peine distinct même à fort grossissement, avec de rares points peu profonds et espacés, alignés près des stries, le huitième assez densément ponctué au côté externe.

Dessous brillant, à pubescence presque nulle ; *proépisternes* à ponctuation limitée au côté interne ; métépisternes à ponctuation et pubescence denses ; abdomen ponctué-chagriné seulement latéralement.

J'ai vu le type de cette espèce, qui est conservé au British Museum (Natural History), à Londres. Il provient du NIGERIA : Old Calabar et je ne connais pas d'auter point de capture.

13. **Epomis jordani** sp. n.

Long. 18 mm.—Tête d'un vert métallique, le labre ferrugineux, les mandibules d'un brun foncé ; pronotum d'un bleu verdâtre moins métallique que la tête, avec des reflets violacés sur le disque ; élytres d'un violet pourpré particulièrement éclatant ; dessous brun de poix, plus clair au milieu ; palpes, antennes et pattes d'un ferrugineux clair, les tarses un peu plus foncés. Pilosité du dessus très faible.

Tête courte et large, modérément épaissie en arrière ; bord antérieur du labre subdroit ; surface à ponctuation grosse et espacée, le milieu du front imponctué ; dernier article des palpes faiblement dilaté.

Pronotum à peu près aussi large que long, non transverse, très peu convexe, nettement élargi en avant et subcordiforme ; largeur maximale située dans le tiers antérieur ; bord antérieur subdroit, les angles légèrement avancés en lobes, arrondis au sommet ; côtés modérément arqués en avant et en arrière de la largeur maximale, puis rétrécis et rectilignes jusqu'aux angles postérieurs qui sont sub-droits et modérément arrondis ; base droite, à côtés à peine obliques, plus étroite que le bord antérieur ; dépressions basilaires profondes et très allongées, sub-linéaires dans le fond, à peine obliques ; surface couverte d'une ponctuation assez grosse mais très espacée, un peu plus dense le long du sillon longitudinal médian et près de la base. *Elytres* allongés et ovoïdes, à largeur maximale située dans le second tiers, modérément convexes ; stries profondes mais assez étroites, à ponctuation bien distincte ; intervalles assez convexes mais nullement tectiformes, à microsculpture particulièrement fine et serrée, imponctués au milieu mais avec une rangée de points assez gros et très rapprochés le long des stries, le huitième intervalle entièrement ponctué, les points plus rapprochés dans la partie externe.

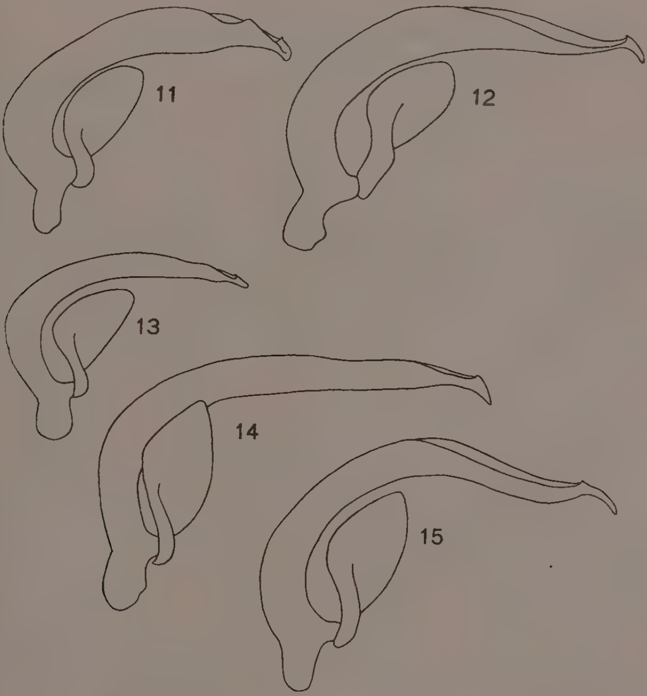

Fig. 11 à 15.—Edéages. (11) *Epomis jordani* sp. n. (Kigonsera). (12) *E. elisabethanus* Burgeon (Ganza). (13) *E. caffer* Boheman (Bulawayo). (14) *E. lasti* Bates (Tanga). (15) *E. elongatus* Klug (Ankovana). × 10.

Dessous à ponctuation et pubescence limitées ; *proépisternes* ponctués seulement dans la partie interne ; métépisternes, plus courts que chez les autres espèces et plus densément ponctués que les proépisternes ; abdomen légèrement ponctué-chagriné sur les côtés. *Edéage :* fig. 11.

Tanganyika Territory : Kigonsera, 1912 (*Max Körner*). Un seul ♂, au Musée Royal du Congo Belge à Tervuren.

Je suis heureux de dédier cette espèce à Monsieur Karl Jordan, en témoignage de profonde estime et de grande sympathie.

14. *Epomis elisabethanus* Burgeon.

Burgeon, 1935, *Bull. (Ann.) Soc. ent. Belg.* 75 : 50 ; 1935, *Ann. Mus. Congo Belge*, sér. in-4°, Zool. 3, 2, *Carab.* : 234. Basilewsky, 1953, *Explor. Parc nat. Upemba*, **10**, *Carab.* : 132.

Long.—17–20 mm.—Dessus entièrement d'un violacé pourpré, l'avant-corps souvent un peu plus vif ; labre ferrugineux ; mandibules d'un brun foncé ; dessous noir de poix, sans reflets métalliques ; palpes, antennes et pattes d'un ferrugineux rougeâtre, les tarses plus foncés.

Tête large, fortement épaissie en arrière ; bord antérieur du labre droit ; ponctuation de la surface faible, laissant tout le front lisse. Palpes longs, le dernier article des labiaux et des maxillaires faiblement dilaté à l'extrémité, un peu plus chez le mâle que chez la femelle.

Pronotum un peu plus long que large, modérément convexe, à largeur maximale située presque au milieu de la longueur ou un peu déportée en avant du milieu ; bord antérieur droit, les angles antérieurs peu marqués et non avancés ; côtés légèrement arqués d'abord, puis rectilignes jusqu'aux angles postérieurs qui sont sub-droits et moyennement arrondis, situés sur le même niveau que le milieu de la base ; cette dernière de même largeur que le bord antérieur ; dépressions basilaires profondes et allongées, un peu obliques, linéaires dans le fond. Surface à ponctuation faible et rare, les points particulièrement espacés. *Elytres* subovoïdes, à largeur maximale située dans le second tiers ; stries fines et profondes, modérément ponctuées ; intervalles convexes, à microsculpture isodiamétrale très serrée, de chaque côté des stries une rangée de points superficiels et assez espacés, le huitième intervalle à ponctuation dense au côté externe.

Dessous à pubescence presque nulle ; *proépisternes* avec des points très isolés dans la partie interne ; métépisternes à ponctuation dense mais peu profonde ; côtés de l'abdomen fortement ponctués-chagrinés. *Edéage :* fig. 12.

Type au Musée Royal du Congo Belge à Tervuren.

E. elisabethanus est répandu au Congo Belge (Kivu et Katanga), en Uganda, ainsi que dans une partie du Southern Rhodesia ; je ne la connais pas du Northern Rhodesia, mais il doit certainement y exister. Cette espèce présente une race méridionale, que je décris plus loin, et qui est spéciale à la partie Sud du Southern Rhodesia.

Congo Belge : Kivu : Haute Luvubu, territ. d'Uvira, 2750 m., dans l'humus, v.1954 (*N. Leleup ;* MRCB). Lualaba : P. N. Upemba, Mukana, 1810 m., iv.1947, i.1948, x.1948 (*Miss. de Witte*), P. N. Upemba, Lukawe, 700 m., ii.1948 (*id.*), P. N. Upemba, Lusinga, 1760 m., xii.1947 (*id.*), P. N. Upemba, Kaziba, 1320 m., iv–v.1948 (*id.*), P. N. Upemba, Munoi, 890 m., vi.1948 (*id.*), P. N. Upemba, Masombwe, 1120 m., x.1948 (*id.*), P. N. Upemba, Ganza, 860 m., vi.1949 (*id.*), Kando près Mutaka, viii–x.1953 (*R. P. Th. de Caters ;* MRCB). Haut Katanga : Elisabethville, vii.1920 (*P. Sporcq ;* MRCB).

Uganda : Lac Victoria-Nyanza, I. Ukerewe, i.1937 (*R. P. Conrads ;* MRCB).

Southern Rhodesia : Cloudlands, Vumbu Mts., 6000′ (South. Rhod. Mus. ; MRCB).

Les spécimens de l'Uganda et de la Haute Luvubu sont identiques à ceux du Katanga. Les exemplaires du Parc National de l'Upemba sont conservés à l'Institut des Parcs Nationaux du Congo Belge et au Musée Royal du Congo Belge à Tervuren.

E. elisabethanus **bulawayanus** subsp. n.

Long. 16–19 mm.—Diffère de la forme nominale par la coloration : dessus noirâtre, avec de forts reflets bleutés violacés sur la tête et le pronotum, presque nuls sur les élytres. La ponctuation du pronotum est formée de points plus gros et encore plus espacés. L'*édéage* est presque identique à celui d'*elisabethanus.*

SOUTHERN RHODESIA : Bulawayo (3 ex., dont l'holotype, au Musée Royal du Congo Belge à Tervuren).

15. *Epomis caffer* Boheman.

Boheman, 1848, *Ins. Caffr.* **1** : 158. Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 181. Péringuey, 1896, *Trans. S. Afr. phil. Soc.* **7** : 491, 514 ; 1926, *Ann. S. Afr. Mus.* **23** : 584, 589.

simba Alluaud, 1929, *Bull. Soc. ent. Fr.* **1929** : 253 (**Syn. nov.**).

caffrarius Csiki, 1931, *Col. Cat.*, pars 115 : 990.

Long. 17–20 mm.—Dessus métallique très vif, variant du bleu verdâtre clair au violet, l'avant-corps parfois un peu plus clair ; labre ferrugineux ; mandibules d'un brun foncé ; dessous noir de poix, un peu plus clair au milieu, à irisation à peine distincte sur les côtés ; palpes, pattes et antennes d'un ferrugineux rougeâtre. Pilosité du dessus presque nulle. Forme plate et assez large, le pronotum et les élytres particulièrement déprimés.

Tête allongée et modérément large, rétrécie en arrière des yeux où les tempes sont presque étranglées ; bord antérieur du labre fortement échancré ; surface faiblement ponctuée, tout le front lisse. Dernier article des palpes fortement élargi chez les deux sexes, surtout aux labiaux.

Pronotum plus large que long, nettement transversal, très déprimé, fortement élargi en avant, subcordiforme ; largeur maximale située dans le tiers antérieur ; bord antérieur droit, les angles antérieurs peu marqués ; côtés fortement arrondis en avant, puis rétrécis et subrectilignes jusqu'aux angles postérieurs qui sont largement arrondis et situés plus en avant que le milieu de la base ; cette dernière plus étroite que le bord antérieur ; dépressions basilaires profondes et allongées, sublinéaires dans le fond ; surface à ponctuation particulièrement rare et espacée. *Elytres* très déprimés, faiblement subovoïdes, à largeur maximale située dans le tiers postérieur ; stries fines et profondes, nettement ponctuées ; intervalles plans, avec une rangée de points faibles mais assez nombreux alignés le long des stries, à microsculpture isodiamétrale très fine et serrée, le huitième intervalle avec des points supplémentaires au côté externe.

Dessous à pubescence très faible mais à ponctuation abondante ; *proépisternes* assez grossièrement et régulièrement ponctués ; métépisternes à ponctuation dense ; côtés de l'abdomen fortement ponctués-chagrinés. *Edéage :* fig. 13.

J'ai pu examiner le type de Boheman, conservée au Musée de Stockholm, ainsi que celui de *simba* Alluaud, qui se trouve au Muséum de Paris. La synonymie donnée plus haut ressort clairement de cette comparaison. D'autre part, le nom nouveau de *caffrarius* proposé par Csiki par suite d'une homonymie présumée avec *Chlaenius caffer* Boheman (1848, *l.c.* : 145) est inutile, l'espèce qui nous occupe ici ayant été décrite dans le genre *Dinodes* et non congénérique avec la seconde.

E. caffer est répandu en Rhodésie du Sud et au Transvaal, et a été retrouvé dans le Sud de l'Angola et au Kenya.

Transvaal : In montibus Makkaliensibus (Mus. Stockholm). Southern Rhodesia : Salisbury (SAM), Bulawayo, x.1929 (*R. H. R. Stevenson ;* coll. Straneo ; *id.*, i.1929, MRCB), Gatooma, 1943–46 (*De Vendictis ;* coll. Boldori ; MRCB). S. Angola : Mungobi, 50 mls. W. Namakunde (*C. Koch ;* MRCB).

Kenya : Nairobi, iv.1924 (*van Someren ;* MP).

16. *Epomis lasti* Bates (fig. 16).

Bates, 1886, *Ent. mon. Mag.* **23** : 11. Kolbe, 1897, *Käfer D.O. Afrika* : 68. Burgeon, 1935, *Bull. (Ann.) Soc. ent. Belg.* **75** : 49 ; 1935, *Ann. Mus. Congo Belge*, sér. in-4°, Zool. **3**, 2, *Carab.* : 234 ; 1937, *l.c.* : 399. Basilewsky, 1953, *Explor. Parc Nat. Upemba, Mission de Witte*, **10**, Carab. : 133.

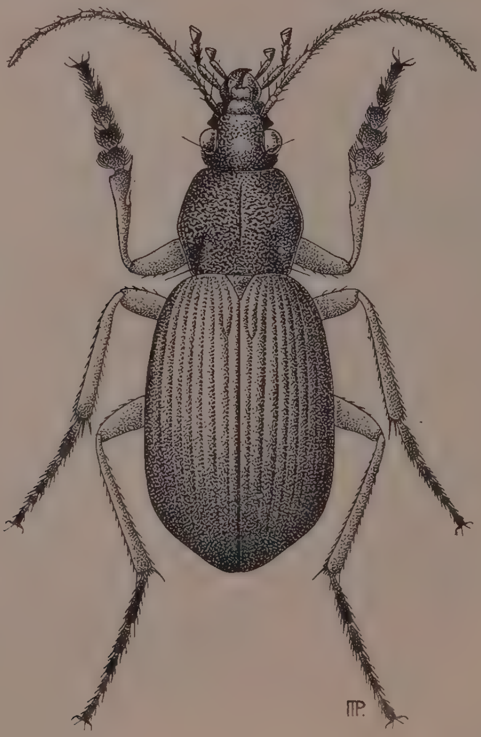

Fig. 16.—*Epomis lasti* Bates (Kafakumba). × 35.

Long. 23–26 mm.—Tête et pronotum noirs, ce dernier avec de légers reflets violacés sur les côtés ; écusson noir ; élytres d'un violet bleuté vif, noirs à la base ; labre ferrugineux foncé ; mandibules noirâtres ; dessous brun de poix foncé, le dernier segment abdominal étroitement bordé de ferrugineux ; pattes, palpes et antennes d'un ferrugineux rougeâtre ou testacé. Quelques rares exemplaires ont les élytres bleus foncés, sans reflets violacés. Pilosité du dessus fine et rare.

Tête grosse et large, fortement épaissie en arrière des yeux ; bord antérieur du labre échancré ; ponctuation particulièrement grossière et dense sur toute la surface, sauf au milieu du front. Dernier article des palpes maxillaires et labiaux fortement sécuriforme chez le mâle, à bord antérieur aussi large que la moitié de la longueur totale de l'article, moins dilaté chez la femelle.

Pronotum pas plus large que long, non transverse, modérément convexe, à largeur maximale située au milieu de la longueur ; bord antérieur droit, les angles antérieurs peu marqués ; côtés régulièrement et faiblement arqués, puis rectilignes en arrière jusqu'aux angles postérieurs qui sont largement arrondis et faiblement prolongés en lobes ; base droite au milieu, de même largeur que le bord antérieur ; dépressions basilaires profonds et sub-allongées, obliques ; surface à ponctuation particulièrement grosse et rapprochée, donnant un aspect couturé. *Elytres* larges et subovoïdes, à largeur maximale située en arrière du milieu ; stries étroites et profondes, ponctuées ; intervalles bombés, les 3, 5 et 7 un peu tectiformes, tous couverts d'une ponctuation dense et assez forte, les impairs présentant une étroite ligne longitudinale médiane lisse.

Dessous à pubescence faible mais à ponctuation forte ; *proépisternes* à ponctuation grosse et assez régulière ; métépisternes à ponctuation plus dense et plus fine ; abdomen avec quelques points sur les côtés. *Edéage :* fig. 14.

Le type de Bates se trouve dans la collection Oberthür, au Muséum National d'Histoire Naturelle de Paris.

Cette espèce n'est connue que du Tanganyika Territory et du Sud-Est du Congo Belge.

TANGANYIKA TERRITORY : Mpwapwa (MP, type), Tanga (MP, MRCB), Ndanda (Mus. Munich), Namupa (Mus. Munich), Lukuledi (Mus. Munich), Kigonsera (Mus. Munich).

CONGO BELGE : Tanganika : Moba, i.1933 (*L. Burgeon ;* MRCB), Haut-Katanga : Katompe, ii.1935 (*Ch. Seydel*). Lualaba : Kafakumba, xii.1931, ii.1933 (*F. G. Overlaet ;* MRCB), P. N. Upemba, Kaswabilenga, x.1947 (*Miss. de Witte*, Inst. Parcs Nat. Congo Belge), P. N. Upemba, Kateke, 950 m., xi–xii.1947 (*id.*, *id.*, MRCB), P. N. Upemba, Kaziba, 1140 m., ii.1948 (*id.*, *id.*), Munoi 890 m., vi.1948 (*id.*, Inst. Parcs Nat. Congo Belge, MRCB), P. N. Upemba, Kilwezi, 750 m. NYASALAND : Blantyre (BM), viii–ix.1948 (*id.*, Inst. Parcs Nat. Congo Belge).

17. *Epomis elongatus* Klug.

Klug, 1833, *Abh. Akad. Wiss. Berlin* : 129. Chaudoir, 1876, *Ann. Mus. Stor. nat. Genova* **8** : 127. Jeannel, 1949, *Faune Emp. franç.* **11**, *Col. Carab. rég. malg.* : 798, 799.

Long. 17–18 mm.—Tête verte foncée métallique ; pronotum et élytres noirs, le premier avec de forts reflets verts métalliques sur les côtés ; labre ferrugineux-testacé ; mandibules brunes ; dessous brun de poix, plus clair au milieu, le dernier segment abdominal étroitement bordé de ferrugineux ; épipleures des élytres ferrugineux ; palpes, pattes et antennes ferrugineux. Pilosité du dessus faible et rare.

Tête courte et large, fortement épaisse en arrière ; bord antérieur du labre sub-droit ; surface très éparsement ponctuée, tout le front lisse. Dernier article des palpes labiaux et maxillaires faiblement dilaté, pas plus élargi chez le mâle que chez la femelle, le bord antérieur bien plus étroit que la moitié de la longueur totale de l'article.

Pronotum un peu plus large que long, à peine transversal, modérément convexe ; largeur maximale déportée en avant du milieu ; bord antérieur droit, les angles antérieurs moyennement marqués ; côtés modérément mais régulièrement arqués, rectilignes en arrière jusqu'aux angles postérieurs qui se trouvent à peu près au niveau du bord postérieur ; base de même largeur que le bord antérieur ; dépressions basilaires profondes et allongées, obliques, surface à ponctuation très espacée et rare, les points profonds et assez gros. *Elytres* ovoïdes, assez convexes, à largeur maximale située en arrière du milieu ; stries profondes et modérément étroites, finement ponctuées ; intervalles pareillement bombés, les 5 à 7 premiers pourvus d'une ponctuation concentrée latéralement, laissant une bande médiane lisse, 8 et 9 densément et régulièrement ponctuées.

Dessous à pubescence et ponctuation faibles et rares ; *proépisternes* pourvus de gros points dans la partie interne ; métépisternes à ponctuation dense et régulière ; abdomen peu ponctué latéralement. *Edéage :* fig. 15.

Le type d'*elongatus* se trouve au Musée de Berlin ; celui d'*epipleuralis* au Muséum de Paris. R. Jeannel a déja signalé cette synonymie.

MADAGASCAR : Région des Antsihanaka (*Perrot*, MP), Farafangana (*R. P. Blucheau ;* MP), Maroansetra (Inst. roy. Sci. nat. Bruxelles), Ankovana, viii, 1945 (*J. Vadon ;* MRCB).

ZOOGEOGRAPHICAL SIGNIFICANCE OF DISTRIBUTIONAL CHANGES IN BRITISH MACROLEPIDOPTERA.[1]

By Bryan P. Beirne.[2]

The distributions of the British species of macrolepidoptera were used as one of the bases on which the origins and histories of the species as inhabitants of the British Isles were reconstructed (Beirne, 1947). It was suggested by Downes (1948) that because the distributions of some species of butterflies have undergone major changes within the past 150 years these distributions are not a reliable basis for zoogeographical theories on those species. Macan (1953) amplified this suggestion into a statement and apparently extended it, without quoting supporting evidence, to cover the entire British macrolepidoptera. The extent and probable causes of the known distributional changes indicate that the distributions of the species concerned can be used as a reliable basis for the construction of historical theories.

Extinctions of existing populations and appearances of new populations may be classified into two main groups: those that can be correlated with environmental changes directly or indirectly caused or initiated by man, and those in which human agency has played no apparent part. The former are not of concern in the present discussion as allowance is made for them in the construction of historical theories; known migrants are also excluded from this discussion. Natural distributional changes, which are discussed here, are of importance in zoogeographical theories. However, though the changes discussed have not been correlated with human activities in some instances human agency may possibly have operated in ways as yet unrecognised.

Small scale natural distributional changes—mostly local extinctions—of British macrolepidoptera are known to have occurred (Beirne, 1955) from the effects of weather, natural enemies, and vegetational changes that were not caused or influenced by human influence or its cessation. The frequency of the occurrence of natural extinctions and colonisations is debatable. It is usually difficult, and often impossible, to distinguish between apparent and real temporary extinctions. That a species was not seen in a situation for a few years does not necessarily mean that it was temporarily extinct there, and the appearance of a species in a situation does not necessarily mean that it has not always been in the habitat of which that situation is a part. Temporary disappearances, or the appearances of species not seen previously, are commonplace in every locality no matter how intensively it is worked. Williams' (1939) figures provide an illustration of apparent changes: only 45 per cent. of the total number of species captured in light traps in four years were captured in all four years; 23 per cent. were captured in three of the four years, 13 per cent. in two, and 19 per cent. in one.

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Such local changes are probably caused primarily by movements of the breeding sites from one part of a habitat to another, i.e., nearer to or farther from the collecting site, combined with seasonal fluctuations in the abundance of the species. Collecting in any situation will produce species that have bred in that situation together with specimens that have wandered from other breeding grounds nearby. The numbers of any of the latter depend on the distance of the breeding ground from the collecting site in relation to the flight habits of the species, and on the relative abundance of the species in its breeding-grounds: the greater its abundance the larger the number of specimens likely to wander into the surrounding areas. If the species becomes relatively scarce for a time, few specimens may stray from the breeding-grounds and none may be captured in nearby situations, giving the impression that it has died out in the latter.

It seems probable that some species may be apparently rare because effective collecting methods have not been used in the breeding-grounds at the right times. Recorded captures may have been made largely in the fringe areas. Examples are species such as *Leucodonta bicoloria* Schiffermüller, *Roselia aerugula* Hübner, *Hadena dysodea* Schiffermüller, *Apamea pabulatricula* Brahm, *Apatele strigosa* Schiffermüller, *Epicnaptera ilicifolia* L., *Catocala fraxini* L., *Cleora arenaria* Hufnagel, *Sciapteron tabaniformis* Rottemburg, and *Parascotia fuliginaria* L. (Bretherton, 1951). These are species that may have disappeared from known breeding-grounds, usually indirectly from human agency, but that probably are still inhabitants of the British Isles in localities that have yet to be discovered, or at least recorded. Lack of captures of " rare " species more probably indicates inadequacy of collecting methods rather than that the species are actually excessively rare. The apparent appearances in recent years of, for example, *Sedina büttneri* Hering, *Phoberia lunaris* Schiffermüller, and *Calamia tridens* Hufnagel, are probably the result of collecting in localities previously unworked at the right times, or collecting by new methods, possibly combined in some instances with temporary increases in the abundance of the species in question. Possibly these and similar species have always been inhabitants of the British Isles.

Movements of the breeding-grounds from one part of an isolated area of the habitat to another are probably commonplace. They can take place gradually, and there is little to prevent them. The colonisation of isolated areas of habitat from others is a different matter, as there are many factors that tend to prevent it, and the extent of the colonisations or recolonisations cannot be estimated. There are many factors involved, and these vary with each species. Though in theory the distance a species can spread from its breeding-grounds is the distance it can fly assisted by wind, in practice this distance is greatly reduced, except with migrants, by a number of factors.

There are inducements for the species to remain at their breeding-grounds and little or no inducements for them to leave. Attractants in the forms of flowers and other food baits, individuals of the opposite sex, and larval food plants are usually present at or near the breeding-grounds, but are usually absent or less concentrated elsewhere. Many species are sedentary in habits and apparently always remain at their breeding-grounds. The fact that most species apparently have not been captured any appreciable distance from suitable breeding-grounds indicates that their dispersal may be a relatively rare occurrence ; such captures are usually subject to comment and have been recorded for some species, for example, *Actebia praecox* L. and *Lycophotia porphyrea* Schiffermüller. To establish new colonies, or re-establish extinct ones, the gravid females must spread. There is plenty of evidence, from light-trap and other collecting data, that in most species the female flies much less than the male. The indications are that the flight activities of the females of most species are largely connected with feeding and egg-laying. There is usually no incentive for the female to leave the breeding-grounds for these purposes. The smaller the population of a species the less the likelihood that some specimens will wander from the breeding-ground.

When a species leaves its breeding-ground its dispersal is obstructed by various barriers. Distance can be an effective barrier : the distance between suitable habitats may be too great for the species to spread from the one to the other. The likelihood of its spreading in this way must decrease progressively with increasing distance. The more specialised the habitats of a species the fewer these habitats are likely to be in number, and consequently the greater their distance apart and the lesser the likelihood of a species colonising the one from the other. The fen, marsh, and reedswamp species, whose habitats are isolated, provide evidence of this (Beirne, 1953). The importance of topographical barriers is obvious from the tendency of most Lepidoptera to fly along the side of such a barrier, for example, a hedge or ridge, rather than to fly over it. Ecoclimatic barriers are, however, probably the chief obstacle to dispersal. Their effectiveness may be deduced from the strong influence of weather conditions on the activities of Lepidoptera, from the extensive variations in ecoclimatic conditions from situation to situation, and from the extensive differences in sizes of populations in different situations. There are indications that, for example, even a river is a highly effective barrier to dispersal, possibly because the air over its surface is cooler than that over its banks (Beirne and Harris, 1946).

Because a species can reach a new locality where environmental conditions are suitable for its survival does not always mean that it can establish itself there readily or at all. The mortality of all stages is normally heavy (e.g., Beirne, 1955). Therefore, the chances of a species establishing itself in a new locality may normally be small, unless it arrives in sufficient numbers and concentration to produce a population sufficiently large for an adequate number to survive. The chances of its arriving in such numbers, or the chances of the progeny of one or a few females surviving in sufficient numbers to produce a permanent population, does not appear to be strong. However, this does not invariably apply. A relatively large proportion of the progeny may survive if some of the important natural enemies in the normal home of the species are absent from the newly colonised areas. For example, it was suggested that the great increase in the abundance of *Yponomeuta rorella* Hübner shortly after its establishment in England was due to arrivals without their normal parasites, and this view was supported by the low rate of parasitism (Fryer, 1937). Species that have specialised habits and a smaller number of effective natural enemies may be able to establish themselves more readily in new localities than species that are controlled by a larger number of natural enemies that are not host-specific.

Species of Lepidoptera that normally fly only when the sun is shining, and they comprise about 10 per cent. of the total, appear to be less affected by ecoclimatic barriers than the remainder. A possible reason for this is that the temperature in the sunshine is high as compared with that in the shade or after sunset. Consequently the chill factor—that moving air feels colder than still air of the same temperature—produced by wind in the sunshine is much lower, and may in practice be so low as not to affect the insects. Largely because of this, wind probably has a much less restrictive effect on the flight and dispersal of diurnal than of crepuscular or nocturnal species. Similarly, conditions of humidity vary greatly from situation to situation and may act as effective barriers to the spread of crepuscular and nocturnal species. Sunshine, however, blankets large areas and may reduce or obliterate the effectiveness of humidity as a barrier to the dispersal of diurnal Lepidoptera.

The majority of the species of Lepidoptera that are known to have undergone natural major distributional changes are day flying and sun loving. Most of the best examples are butterflies. There are other species that have undergone major distributional changes that were caused or facilitated by human agency. For instance, some Fenland species have been reduced in abundance or caused to become extinct primarily by the destruction or alteration of their habitats by man (Bretherton, 1951); others have been spread or have been enabled to spread by planting of their food plants. Most conifer feeding species and the delphinium feeding species, *Polychrisia moneta* F., are examples of the latter.

Species that have definitely undergone major distributional changes in which human agency has apparently played no significant part fall into several groups on a basis of the times when the main changes took place. In some instances possible basic causes of the changes can be indicated tentatively by correlating their times of occurrence with weather trends. The distributional changes have been recorded in a large number of papers and notes in entomological periodicals, particularly in the past twenty years.

Apparently no weather trends are known that can be correlated with the major reductions in the abundance and contractions of the distributions of *Polygonia c-album* L. and *Cyaniris semiargus* Rottemburg and possibly of *Limenitis camilla* L., *Argynnis paphia* L., and *Nymphalis io* L., which took place mainly between about 1840 and about 1870. *C. semiargus*, which occurred as isolated populations and which may have been affected by the introduction of mechanical methods of hay cutting, eventually became extinct. *P. c-album* began its remarkable recovery in 1921, and the less spectacular recoveries of *L. camilla* and *A. paphia* apparently started about the same time. *N. io* began its recovery in the early 1930's. The appreciable increase in the average temperatures of spring, summer, and autumn since 1930 (Manley, 1952) may have been the primary cause of the recovery of *N. io*, but likely reasons for the recoveries of the three remaining species cannot be suggested. There are slight indications that sunshine or summer temperature may have been an important factor. These are sun-loving insects, they have their centres of distribution in the British Isles in southern England—the warmest, driest, and sunniest part of the country, and in 1921, the year their recoveries started, the summer was very long, hot, and sunny. The fact that the early years of their recovery coincided with a period of relatively high rainfall may indicate that moisture was of little significance.

The next species to undergo marked reductions in abundance and distributions were *Aporia crataegi* L. and *Apamea pabulatricula* Brahm, whose major period of decline was between about 1860 and the 1880's, and which eventually became apparently extinct as inhabitants of the British Isles, according to published records. There was an apparent downward trend in temperature, particularly in winter, between 1850 and 1885 and the summer rainfall was relatively high from 1871 to 1880. These factors, particularly the latter, may have been the primary causes of the declines. There are some supporting indications. The view has been put forward that the decrease of *A. crataegi* was caused by a succession of wet summers and mild winters, and in the New Forest the species gradually became scarce after the very wet summer of 1871 and died out in 1880. These species may have become extinct because they occurred as isolated populations that died out one after the other. Human agency—pollution of the foliage with industrial fumes (*A. pabulatricula*) and spraying of fruit trees (*A. crataegi*)—may have had some influence on the disappearances.

The remarkable decline of *Pararge aegeria* L. took place between about 1870 and about 1910. There are indications that the spectacular recovery of the species may have begun in the middle 1920's (Downes, 1948), though it did not start on a large scale until the early 1930's. There are indications that rainfall trends may have been the primary causes of the fluctuations of *P. aegeria*. It is an insect that, though sun-loving, mainly frequents damp, shady situations. It was relatively common in wet summers, as in 1879 and 1892, and relatively scarce in dry summers, as in 1870 and 1887. During its period of decline it always remained widely distributed and locally common in those parts of the British Isles—Ireland and the western parts of Great Britain—where the average rainfall is high, whereas it disappeared from the drier, south eastern and eastern parts of Great Britain. Though the beginning of its decline coincided with a period of relatively high summer rainfall, 1871 to 1880, the main part of the decline coincided with relatively dry periods: dry summers predominated from 1884 to 1893, the summers from 1894 to 1910 had, on the average, about average rainfall, and those from 1907 to 1916 were moderately dry (Glasspoole, 1941). Its recovery began during a period of wet summers, 1923–1932, and its first major reappearances occurred in 1931, which was one of the wettest summers, with 1924 and 1927, of the preceding fifty (1932, British Rainfall Organisation, pp. 2–4) and a bad year for most species of butterflies. The recovery continued during the 1930's and 1940's, when there was no appreciable trend toward wetness or dryness though there was an appreciable increase in the average temperatures of spring, summer, and autumn. There is some evidence that during its recovery this species was less confined to damp, shady situations than formerly. Increased rainfall, by making formerly unfavourably dry situations suitably moist, may account for this. In the western, or wetter, parts of its range in the British Isles it is not infrequently an inhabitant of open country.

Leptidea sinapis L. underwent corresponding distributional changes simultaneously with *P. aegeria*, though the changes were much less extensive. Its distribution in the British Isles indicates that relatively high rainfall is not harmful and the species, like *P. aegeria*, frequents moist, shady situations. These points, together with the coincidence of its decline and recovery with those of *P. aegeria*, indicate that its distributional changes may have had the same basic cause.

At the beginning of the present century *Nymphalis polychloros* L. and *Hadena dysodea* Schiffermüller disappeared from wide areas, apparently rather suddenly. On a smaller scale, the same apparently happened to *Pararge megera* L. and *Eulype hastata* L., though the exact date of the local disappearances of the latter is not clear, and *Maniola jurtina* L. underwent some local extinctions. Except *H. dysodea*, which, probably because its numbers were too severely reduced, has not undergone a significant recovery, these species increased in abundance and recovered their lost ground in the 1930's and 1940's. Temperature may have been the basic factor that affected these species. The cold summers of 1902 and 1903, of which the latter was also very wet, seem to have been the times when the disappearances occurred, at least with *N. polychloros* and *M. jurtina*; the exact dates of the disappearances of the remaining species are not clear, but they seem to have been about those years. Less extensive, local disappearances of some other species of butterflies—*Aglais urticae* L., *Coenonympha pamphilus* L., and *Erebia aethiops* Esper—occurred in those years. The recovery of the species occurred during the period when there was an appreciable increase in the average temperatures of spring, summer and autumn. This temperature trend may also have been responsible for the distributional extensions northward of *Sphinx ligustri* L., *Gastropacha quercifolia* L., and *Catocala nupta* L. that seem to have taken place in the 1930's and 1940's.

There are factors additional to the relative ineffectiveness of climatic barriers that facilitate the dispersal of the species discussed above. Some of the species are known to be capable of sustained flights: *N. io*, *M. jurtina* and *P. megera* are known to undertake overseas flights. With these species winds assist instead of preventing dispersal, as butterflies, unlike most moths, will fly in moderate and even in relatively strong winds if conditions of sunshine and temperature are suitable. Diurnal species apparently find flowers and mate largely by sight when in flight. This contrasts with most moths, for which odours emitted by the foodstuffs and by the unfertilized resting females appear to be the primary attractants. Finally, dispersal of the species of butterflies whose distributions have expanded is favoured by their courtship flights (Temple, 1949) whereas the courtship activities of the great majority of moths apparently take place while the female is at rest.

The foregoing shows that species that undergo major natural distributional changes are exceptional among the British species of Macrolepidoptera in that they comprise only a very small minority of the total. The species mentioned are all that, so far as can be discovered, are definitely known to have undergone major natural distributional changes. They comprise under 3 per cent. of the total. The distributions of some other species may fluctuate, but to a lesser extent. The apparent colonisations of the Salisbury area by *Rhyacia simulans* Hufnagel and of the Isle of Man by *Euchloe cardamines* L. in recent years are rather extreme examples. It seems not improbable that minor distributional changes may be regular occurrences with relatively common and widely distributed species, i.e. species that occur as single or contiguous populations over wide areas. With increasingly local distributions, i.e., greater isolation of populations, decreasing abundance, and more sedentary flight habits such distributional changes must become increasingly less frequent. With most species such changes are probably exceptional, and with a great many their occurrence may be so infrequent as to be negligible in practice.

The major natural distributional changes have probably been caused by long term weather fluctuations. These distributional changes, caused by weather, are fluctuations about means that are determined by climate. Persistent changes in the mean for any species, other than changes directly or indirectly assisted by man and those that reach the ultimate limit of extinction, are caused by climatic changes. For example, the increasing climatic warmth of the early Postglacial permitted the spread of some species whose ranges had been limited during the Last Glacial Phase, and the climatic deterioration after the Postglacial climatic optimum reduced the ranges of others (Beirne, 1947). The concept of distributional fluctuations, when they occur, caused by weather about means determined by climate enables the known distributions to be used as a reliable basis for the construction of historical theories.

Acknowledgment.

I wish to thank Mr. J. A. Downes, Medical and Veterinary Entomology Unit, Entomology Division, Department of Agriculture, Ottawa, for suggestions and constructive criticisms.

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" Which are the factors that have brought into existence the fixed characteristics of geographical subspecies? If we have an answer to this question, the mystery of the origin of species is solved. Meanwhile, we must content ourselves with watching what is going on in the greatest biological laboratory, where free access is granted to all who are born into this world. Happy is the man who enters that open door to spend his life among the secret processes in Nature's workshop. I consider myself very fortunate in having found that door."

(Jordan, K., 1931, *Proc. ent. Soc. Lond.* **5** : 142).

" In a period of great economic pressure the clamour of the uninitiated public opinion for applied science might easily warp the judgment of a government and might lead it to decisions which would cripple pure science, forgetting under the stress of the circumstances of the moment that pure research is the indispensable basis of all applied science and that to press for quick results in research is most disastrous, quickly spelling nearly the same as quack."

(Jordan, K., 1931, *Proc. ent. Soc. Lond.* **5** : 128.)

RÉVISION DES ESPÈCES AFRICAINES DU GENRE *EUMETA* WALKER (*CLANIA* AUCT.) (LEPIDOPTERA : PSYCHIDAE).

Par Jean Bourgogne.

Avec 1 Planch et 11 Texte-figures.

Les espèces étudiées dans cet article ont été placées, par les différents auteurs, dans trois genres : *Eumeta* Walker, *Clania* Walker et *Cryptothelea* Duncan. En particulier, Dalla Torre et Strand (1929) les réunissent à d'autres sous le nom générique de *Cryptothelea*, tandis qu'elles figurent dans le genre *Clania* dans les *Macrolépidoptères du Globe* de Seitz (Gaede, 1929). Récemment, J. G. Betrem (1952) a mis de l'ordre dans de nombreux genres des Psychidae en désignant les espèces types, d'où il résulte que le genre étudié ici doit porter le nom d'*Eumeta* Walker (type du genre : *cramerii* Westwood = *layardi* Mr.).

I. Historique.

Les espèces africaines décrites ou citées comme appartenant à ce groupe sont au nombre de huit, plus une " variété " ; on en trouvera la liste presque complète dans l'ouvrage de Seitz (Gaede, 1929).

Or l'étude de la question montre qu'aucune de ces neuf formes ne peut être admise sans discussion, pour des raisons variées qui vont être examinées ; une révision sérieuse s'imposait donc.

(1) *Clania junodis* Conte et Vaney, 1911. Cette espèce est indiquée avec doute comme *Clania* par Gaede in Seitz (p. 484) ; grâce à l'amabilité de M. R. Mouterde, de Lyon, j'ai pu consulter le texte de Conte et Vaney, et constater qu'il s'agit de l'*Eumeta junodi* d'Heylaerts, espèce citée par ailleurs dans le Seitz à la page 484 sous le nom de genre *Acanthopsyche* ; ses caractères morphologiques montrent qu'il ne s'agit pas d'un *Eumeta*. *Clania junodis* est donc à rayer purement et simplement.

(2) *Eumeta ngarukensis* Strand, 1909, du Tanganyika. D'après la structure du fourreau, il s'agit vraisemblablement bien d'un *Eumeta*, mais ce nom n'est pas valide car seul le fourreau est décrit. D'ailleurs, même si le nom était valide, il serait très probablement impossible de reconnaître l'espèce.

(3) *Clania* (?) *guineensis* Strand, 1912, de Guinée Espagnole. Probablement aussi un *Eumeta*, mais espèce à rejeter comme la précédente pour la même raison.

(4) *Eumeta* (?) *salae* Heylaerts, 1884, du Liberia. Espèce transférée dans le genre *Chalia* par Kirby (1892), et maintenue dans ce genre par Gaede in Seitz (p. 486). D'après le fourreau, cette espèce doit aussi être un *Eumeta*.

(5) *Eumeta* (?) *zelleri* Heylaerts, 1884, de Cafrerie (province du Cap). N'est vraisemblablement pas un *Eumeta*.

Ces deux dernières espèces, décrites uniquement d'après le fourreau et la chenille (imago inconnu), sont théoriquement valables. Mais l'absence d'imagos rend actuellement, et peut-être pour toujours, la reconnaissance de ces espèces impossible ; on se trouve donc obligé de ne pas tenir compte de ces deux Psychides.

(6) *Cryptothelea tuckeri* Butler, 1875, de Natal. D'après la description, ce n'est certainement pas un *Eumeta.* Selon l'auteur même de la description, le seul exemplaire qu'il a vu est certainement perdu, et on ne saura probablement jamais avec certitude de quelle espèce il s'agissait ; c'est sûrement pour cette raison que *tuckeri* ne figure pas dans le Seitz.

Les six espèces précédentes doivent donc être écartées. Seules les trois formes suivantes sont à prendre en considération, car elles reposent sur la description des imagos mâles, et il est facile de voir qu'elles appartiennent bien à notre genre. En voici la liste.

(7) *Eumeta cervina* Druce, 1887. Description faite d'après deux exemplaires, l'un de Gambie, l'autre de la Baie Delagoa (Afrique Orientale Portugaise).

(8) *Eumeta moddermanni* Heylaerts, 1888, de la Côte de l'Or. Décrit sur un seul exemplaire mâle.

(9) *E. moddermanni* var. *pictipennis* Strand, 1912, de Guinée Espagnole. Décrit sur sept exemplaires.

Nous allons voir qu'aucune de ces trois formes ne peut être admise sans discussion, car des difficultés s'élèvent à propos de chacune d'elles.

II. ETUDE DU MATÉRIEL.

En vue d'une mise au point de l'ensemble de ces espèces, un matériel relativement abondant a été réuni ; ce matériel m'a été aimablement communiqué par les musées suivants : Carnegie Museum (Pittsburgh), British Museum (Natural History), Rijksmuseum de Leyde, Musée du Congo Belge (Tervuren), Zoologisches Museum de Berlin, Naturhistorisches Museum de Vienne, Instituto Español de Entomologia (Madrid), Department of Agriculture of Salisbury. A ces communications, il faut ajouter la collection du Muséum de Paris, ainsi que les exemplaires confiés ou recherchés à mon intention par plusieurs correspondants. Le nombre d'exemplaires obtenu se monte à 90, nombre très faible en apparence, mais qui représente cependant une grande partie de ce qui doit exister dans les Musées et collections particulières (sauf peut-être en Afrique du Sud) ; de nombreux musées, parfois importants, ne possèdent aucune espèce africaine de ce genre.

L'étude de ce matériel s'est montrée difficile : les caractères morphologiques sont peu tranchés et n'ont souvent qu'une valeur d'ordre statistique ; en particulier, les armures génitales sont peu utilisables, étant presque identiques d'une espèce à l'autre. Il a donc fallu attribuer une importance particulière à l'aspect extérieur : taille, coloration, forme des ailes.

Malgré ces difficultés, il a été possible de grouper la plupart des exemplaires en trois formes distinctes, qui seront considérées comme des espèces :

(1) *Espèce A* (Pl. 1, fig. 5 à 8). Grande taille, ailes antérieures allongées ; Afrique occidentale et équatoriale.

(2) *Espèce B* (Pl. 1, fig. 9 à 12). Presque semblable à A, mais nettement plus petite ; Afrique du sud-est.

(3) *Espèce C* (Pl. 1, fig. 1 à 4). Moins grande que A, ailes antérieures plus courtes, coloration plus sombre ; même répartition que A.

Voici les conclusions, au point de vue nomenclature, résultant de la comparaison de ce matériel avec les trois espèces ou formes décrites : *cervina* Druce, *moddermanni* Heylaerts et *pictipennis* Strand.

(1) *Eumeta cervina* Druce.—La courte description originale est insuffisante, quoiqu'elle contienne certaines indications utilisables. Heureusement, les deux exemplaires originaux ont été conservés (British Museum (Natural History)), mais une difficulté s'élève : l'un de Gambie, appartient à notre espèce A, tandis que l'autre (Delagoa Bay) est de l'espèce B. Voilà donc un cas où les deux exemplaires types n'appartiennent pas à la même unité spécifique, ou au moins subspécifique.

Cette difficulté est facile à lever, par le choix d'un lectotype. Ce choix a déjà été fait pratiquement (mais non publié) par le British Museum, qui a isolé comme lectotype l'exemplaire de Gambie, qui est celui qui répond le mieux à la description originale ; son envergure est exactement celle indiquée par Druce ($1\frac{3}{4}$ in., soit 44,5 mm.), et c'est en même temps l'exemplaire le mieux conservé. L'envergure de l'autre exemplaire, beaucoup plus faible, n'est même pas mentionnée par l'auteur, vraisemblablement en raison de l'état défectueux des ailes qui rend impossible une mensuration exacte. Tout concorde donc pour désigner comme lectotype l'exemplaire de Gambie, et notre espèce A doit donc porter le nom d'*E. cervina* Druce.

(2) *E. moddermanni* Heylaerts.—Le type unique se trouvait au Musée de Stuttgart, mais, comme me l'a écrit le Dr. E. Lindner, il a malheureusement été détruit pendant la dernière guerre ; on doit donc se contenter de la description donnée par Heylaerts, ainsi que des exemplaires de sa collection considérés par lui comme appartenant à la même espèce.

Bien qu'une description datant de cette époque (1888) ne puisse pas remplacer le type, surtout dans un groupe aussi difficile, celle d'Heylaerts est suffisamment bien faite pour qu'on puisse se faire une opinion vraisemblablement exacte sur son espèce : d'une part, celle-ci, provenant d'Afrique occidentale, ne peut être assimilée à celle que j'ai appelée " espèce B ", qui parait complètement étrangère à cette région de l'Afrique ; d'autre part, l'envergure indiquée (38 mm.), la forme " presque triangulaire " des ailes postérieures, certains détails de coloration, ne s'appliquent pas, ou très difficilement, à notre espèce C ; au contraire cette description convient bien à notre troisième espèce, c'est-à-dire à *E. cervina*, et il parait très probable qu'il s'agit bien de *cervina*, espèce très répandue et apparemment peu rare dans ses stations ; Heylaerts considérait *moddermanni* comme distinct de *cervina*, mais il ne dit pas sur quoi il se base, et il semble probable qu'il ne connaissait de *cervina* que la description de Druce.

Quant aux exemplaires qui subsistent de la collection d'Heylaerts et considérés par lui comme identiques à son *moddermanni*, ils ne lui ont été adressés qu'après la rédaction de la description originale (Heylaerts, 1890) et ne peuvent donc pas tenir le rôle de paratypes. De plus, ils proviennent de l'Afrique Orientale Portugaise et appartiennent à notre espèce B, distincte de *cervina*, de sorte qu'il n'est pas possible d'y choisir un lectotype de *moddermanni*, espèce d'Afrique Occidentale. La similitude qui rapproche les deux espèces explique qu'Heylaerts, comme Druce, les ait considérées comme identiques ; seul un matériel abondant permet de voir qu'on a affaire à deux formes bien distinctes, quoique voisines.

Le type étant détruit, il subsistera toujours une petite incertitude sur la véritable identité d'*Eumeta moddermanni* ; cependant la conclusion la plus logique à laquelle on aboutisse, et qui me parait comporter une grande probalité d'exactitude, est qu'il s'agit d'un synonyme d'*E. cervina*.

Onze ans avant la publication de *cervina*, Heylaerts (1876), dans une simple communication, avait annoncé son intention de donner le nom de *moddermanni* à un fourreau de grande taille contenant une chenille, provenant d'Afrique (Libéria) ; il s'agit là d'un nomen nudum, et la description n'est parue qu'en 1888 ; en outre, il ne parait pas possible de savoir si ce fourreau et cette larve étaient bien de la même espèce que le mâle qui a servi à la description. Dans ces conditions, on ne peut pas conserver le nom de *moddermanni*, qui doit disparaître, pour raison de priorité, devant *cervina* Druce, décrit en 1887 ; cette solution offre l'avantage que *cervina* est une espèce bien définie, le type étant conservé, alors que l'adoption du nom d'Heylaerts aurait contenu une part d'arbitraire.

(3) *E. moddermanni* var. *pictipennis* Strand.—Décrit sur sept mâles provenant d'Alén (Guinée Espagnole), dont trois m'ont été communiqués : l'holotype, désigné par Strand dans sa description, et deux paratypes. Ces trois mâles sont assez différents entre eux ; on ne devra donc considérer que l'holotype pour juger de la valeur de cette forme (qui est le seul *Eumeta* africain figuré dans le Seitz, **14**, Pl. 72 h).

Cet holotype ne présente par rapport à *cervina* aucun caractère distinctif bien particulier (Pl. 1, fig. 7) ; c'est un exemplaire de grande taille, bien conservé, à ailes antérieures relativement étroites et à dessins bien contrastés ; la description originale s'applique d'ailleurs très bien à *cervina*. Pourquoi donc Strand a-t-il éprouvé le besoin de créer ce nom de *pictipennis*, apparemment inutile? S'il l'a fait, c'est probablement parce qu'il ne connaissait *cervina* que par la description de Druce ; il précise d'ailleurs, dans sa description, qu'il a comparé ses exemplaires avec des " *moddermanni* " de la Baie Delagoa, donc avec notre espèce B ; la différence entre les deux formes l'a frappé, et l'a engagé à isoler ses exemplaires sous un nom nouveau, ce qu'il n'aurait vraisemblablement pas fait s'il avait eu des *cervina* comme matériel de comparaison.

On est donc tenté de faire de *pictipennis* Strand un simple synonyme de *cervina* Druce. Mais il semble préférable de conserver, au moins provisoirement, le nom de Strand pour désigner les exemplaires de *cervina* à dessins très contrastés, sans d'ailleurs pouvoir préciser s'il s'agit d'une forme individuelle ou raciale.

Les paratypes sont plus petits que l'holotype ; parmi les deux que j'ai examinés, l'un n'est pas un *cervina*, et il en sera question plus loin ; l'autre (Pl. 1, fig. 8) est un petit *cervina* aux ailes antérieures étroites et à angle interne obtus ; il n'est pas sans intérêt de le rapprocher de deux mâles présentant les mêmes particularités, notamment la même envergure, et ayant également des dessins très contrastés, d'autant plus que ceux-ci proviennent de la même région de l'Afrique : Oyem, Gabon (Muséum de Paris), et Fernando Po (Institut d'Entomologie de Madrid).

III. Conclusion de l'Étude Précédente.

Ce qui précède montre que sur huit espèces décrites, une seule est solidement établie, la plus grande partie des autres étant à rejeter définitivement du genre *Eumeta*. On remarque à cette occasion les inconvénients d'une règle rendant valide une description de Lépidoptère basée sur le seul état larvaire.

Il s'agit maintenant de nommer nos deux espèces B et C, et de les définir ainsi que *cervina*. Une étude minutieuse de ces trois séries d'exemplaires accompagnée de mensurations au micromètre portant sur les ailes et sur 22 préparations d'armures génitales et d'abdomens, a permis de dégager quelques caractères spécifiques ; elle a en même temps mis en évidence des caractères communs qu'il n'est pas inutile de noter avant de décrire les espèces.

IV. CARACTÈRES GÉNÉRAUX DES ESPÈCES AFRICAINES DU GENRE *EUMETA*.

Ce qui suit n'est pas une diagnose du genre, mais seulement l'énumération d'un certain nombre de particularités morphologiques.

Les photographies (Pl. 1, fig. 1 à 12) montrent mieux qu'une description l'aspect général, la robustesse du corps, le dessin des ailes qui est très constant, ne différant d'une espèce à l'autre que par le développement plus ou moins grand ou la disparition de certaines taches. La coloration comporte diverses transitions entre le noir (ou brun noir) et le blanc (ou crême), en passant par des tonalités brunes ou gris-brun, parfois brun-rouge ; certaines régions de l'aile antérieure, d'emplacements bien définis, sont translucides ou transparentes par suite du manque d'écailles.

Antennes à article basilaire (scape) très gros, ovoïde, recouvert, ainsi que l'article suivant (pédicelle), d'une longue touffe de poils écailleux d'un jaunebistre souvent clair, mais parfois teinté de brun ; flagelle recouvert d'écailles de teinte claire ; pectinations non écaillées, portant de nombreux cils particulièrement longs disposés en 2 séries divergentes, ces pectinations grêles, à peu près cylindriques, terminées en pointe, les plus longues se trouvant vers le septième article du flagelle. Le nombre d'articles, assez difficile à compter, varie beaucoup, même à l'intérieur d'une même espèce : de 29 à 45 dans l'ensemble du matériel étudié.

Une particularité des antennes du genre *Eumeta* est la présence fréquente d'une ou deux pectinations ramifiées, en forme de fourche (fig. 17) ; cette anomalie s'observe sur près de 40 cent pour des exemplaires étudiés, soit sur une seule antenne, soit sur les deux, presque toujours à la base du flagelle, rarement ailleurs (13e article antennaire) ; cette particularité provient de la soudure partielle de deux (rarement trois) pectinations successives d'une même rangée.

Pattes antérieures ayant une épiphyse sensiblement cylindrique, presque aussi longue que le tibia, légèrement recourbée au voisinage de son extrémité distale.

Pour la nervulation, voir la figure 13 ; elle a déjà été décrite, et Janse (1917) en donne un dessin. On y observe d'ailleurs certaines variations. A l'aile antérieure, 7 est connée avec la tige 8 + 9, ou, moins fréquemment, un peu tigée avec celle-ci. A l'aile postérieure, la nervure 8 (Sc) émet une courte nervure humérale, dont la position par rapport à la " barre " (reliant 8 à la cellule) est assez variable, et les nervures 4 et 5, normalement tigées, sont parfois seulement connées ou même séparées. Ce genre offre une particularité, qui est la présence chez certains exemplaires d'une ou de deux nervures transverses inhabituelles : l'une entre 1 c et 2 de l'aile antérieure, l'autre entre 7 et 8 (au delà de la cellule) de l'aile postérieure ; ces nervures transverses peuvent être complêtes ou partiellement effacées, et leur direction est variable ; elles ont été indiquées sur la fig. 13, mais elles manquent fréquemment.

La forme des sclérites abdominaux (fig. 19 et 20) est un peu variable individuellement ; on remarque que les sternites 3 à 6 ont généralement leurs deux angles latéro-postérieurs plus ou moins aigus, le bord postérieur portant souvent deux petites échancrures, alors que sur les sternites 7 et 8 ces angles sont plutôt obtus ou arrondis, et le bord postérieur non échancré. Les seuls caractères paraissant utilisables pour séparer certaines espèces sont le largeur relative (par rapport à leur longeur) des sternites, notamment de ceux des urites 7 et 8, et la longueur relative des deux pointes latéro-antérieures du 8e.

Armure génitale (fig. 21) ne présentant d'une espèce à l'autre que des variations très faibles, comme c'est le cas dans beaucoup de genres de Psychidae ; la principale variation observée concerne le renflement de la base du processus supérieur (ou costa) des valves, renflement qui tend parfois à former un lobe distinct (pulvillus, terme de Burrows) (p, fig. 18). Pénis de forme constante, renfermant de très nombreux et très petits cornuti transparents en lames de poignard, reconnaissables seulement à un fort grossissement. L'armure génitale est distincte de celle des *Eumeta* des faunes orientale et paléarctique, du moins d'après une série de préparations de quelques espèces asiatiques : un premier caractère est la présence d'un saccus long et grêle chez ces dernières (fig. 23), qui manque dans les espèces africaines, où le tegumen se termine antérieurement par une courbe arrondie ou, plus rarement, une pointe courte ; d'autre part, le vinculum n'a pas la même forme, en ce sens que le point où il atteint son maximum de largeur ne se trouve pas exactement au même endroit : au milieu ou en arrière du milieu de la longueur du vinculum pour l'Afrique (fig. 21), nettement en avant du milieu pour les autres faunes (fig. 23) ; cette dernière constatation a été vérifiée par des mesures prises au micromètre. Reste à savoir si ces deux caractères sont bien constants et s'appliquent à toutes les espèces.

Les femelles et premiers états ne sont bien connus que chez une seule espèce. Quant aux fourreaux, ils ont été souvent décrits, et plusieurs fois figurés (Junod, 1899 ; Strand, 1912 ; Hardenberg, 1919). La variété des matériaux utilisés par les chenilles a donné lieu à la création d'espèces différentes, citées au début de cet article, mais cette variabilité ne parait pas avoir la valeur spécifique qu'on lui a attribuée ; il est prouvé en tout cas qu'une même espèce peut utiliser, suivant les occasions qui se présentent, soit des tiges grossières, soit de longues épines d'*Acacia*, blanches et parfaitement rectilignes. Si les fourreaux sont caractéristiques du genre, il semble qu'on ne puisse guère les utiliser pour séparer les espèces.

Les chenilles servent de nourriture aux indigènes dans certaines régions de l'Afrique (Bergier, 1941 : 68–69).

V. Description des Espèces.

Eumeta hardenbergi sp. n. (Pl. 1, fig. 9 à 12.)

Ce nom pourra désigner l'espèce sud-africaine, c'est-à-dire notre espèce B, en hommage à l'étude détaillée que lui a consacrée C. B. Hardenberg, dans son important mémoire sur les Psychidae de l'Afrique méridionale (1919).

Quoique confondue jusqu'ici avec *cervina*, et citée soit sous ce nom, soit sous celui de *moddermanni*, c'est la seule espèce qui soit parfaitement connue ; c'est pourquoi elle figure ici la première.

Cet *Eumeta*, sous le nom de *Clania moddermanni* Heylaerts, a été décrit d'une façon très détaillée par Janse (1917) et par Hardenberg (1919) ; ce dernier en a étudié et figuré avec grand soin les premiers états et la femelle. C'est également à *hardenbergi* que se rapportent les articles d'Heylaerts (1890) et de Junod (1899). Le mâle a déjà été figuré deux fois, d'abord par Junod, puis par Hardenberg.

L'espèce, déjà bien connue, n'a pas besoin d'être redécrite ici ; ses caractères distinctifs par rapport à *cervina* seront indiqués à propos de ce dernier.

Etant donné l'analogie morphologique qui rapproche *hardenbergi* de *cervina*, on peut se demander si on a bien affaire à deux espèces distinctes, ou seulement à deux sous-espèces d'une même unité spécifique. A la vérité, cette question ne peut guère être tranchée actuellement avec certitude. Cependant certaines considérations, dont l'existence de plusieurs petites différences morphologiques, sont en faveur de la séparation spécifique, et c'est la position qui sera prise ici comme étant apparemment le meilleur.

Les premières indications d'ordre biologique sur cet *Eumeta* ont été publiées par Heylaerts (1890) et surtout par Junod (1899), mais c'est à Hardenberg (1919) qu'on doit la connaissance détaillée de sa biologie ; on ne peut ici que renvoyer à cet important travail. L'espèce est nuisible à différents arbres, surtout aux arbres fruitiers, et pullule certaines années.

E. hardenbergi semble strictement localisé au sud-est de l'Afrique (Natal, Transvaal, Afrique Orientale Portugaise) ; la limite septentrionale connue parait être le Zambèze, mais en réalité elle doit se trouver bien plus au nord, car un exemplaire du Musée de Berlin, provenant de la région de Pangani (N.E. du Tanganyika, Alfr. Reuss), appartient certainement à la même espèce.

Holotype ♂, MOZAMBIQUE : Delagoa Bay, 1891 (H. Deyrolle) (Muséum de Paris). Paratypes, 21 ♂: Mozambique (Heyne) (Musée de Leyde) ; *id.* Junod (id.) ; *id.*, 1900, Heyne (Musée de Vienne) ; Delagoa Bay, coll. de Joannis et Dupont, 3 ♂ (Muséum de Paris) ; *id.*, coll. Neustetter (Musée de Vienne) ; *id.*, 4 ♂ dont 2 provenant du Pasteur Junod (Musée de Berlin) ; *id.*, Joicey coll. (British Museum) ; *id.*, Montero, Joicey coll., paratype de *cervina* Druce (*id.*) ; *id.*, 2 ♂ (coll. F. M. Jones) ; Rikatla, à 24 km. au N. de Lourenço Marques, H. A. Junod, *ex* Oberthür coll., 2 ♂ (British Museum) ; Lourenço Marques, Junod (Musée de Leyde) ; NATAL (Musée de Leyde) ; Pietermaritzburg, viii.1899, P. Richards (British Museum).

Eumeta cervina Druce. (Pl. 1, fig. 5 à 8.)

Les seules articles originaux se rapportant à cette espèce, à part la description de Druce, sont celui d'Heylaerts (1888)—en admettant que son *E. moddermanni* est bien synonyme de *cervina*—et celui de Strand (1912) (*Clania moddermanni* var. *pictipennis*). La publication d'Heylaerts de 1890 (*E. moddermanni*) concerne uniquement *E. hardenbergi.* Dans la répartition donnée par Gaede in Seitz (1929), seule est valable la mention " Gambie " ; les deux autres régions (Delagoa Bay et Afrique Orientale) s'appliquent évidemment à *hardenbergi* ; c'est dans cet ouvrage que se trouve la seule figure publiée du mâle, d'ailleurs assez grossière.

Voici les caractères de *cervina* comparés à ceux d'*hardenbergi* (nombre d'exemplaires étudiés : 30 *cervina*, 25 *hardenbergi*).

Très voisines morphologiquement, les deux espèces différent cependant par une différence de taille très notable : *cervina*, envergure 34 à 47 mm., le plus souvent 39 à 42 mm. ; *hardenbergi*, 29 à 35 mm.

Nombre total d'articles antennaires : *cervina*, 33 à 43 ; *hardenbergi*, 33 à 39. Ce caractère semble sans grande valeur discriminative.

Ecaillement des ailes antérieures paraissant un peu plus dense par endroits, notamment dans les cellules 2–3, 3–4, 4–5 et 7–8, caractère d'ailleurs difficile à apprécier et valable seulement pour les exemplaires en bon état. Forme des ailes identiques en moyenne dans les deux espèces, mais variabilité individuelle plus grande chez *cervina*. Nervures transverses citées précédemment fréquentes seulement chez *cervina* : celle de l'aile antérieure (entre 1c et 2) présente chez 20 exemplaires sur 30, celle de l'aile postérieure (entre 7 et 8) présente chez 7 exemplaires, soit sur une aile, soit le plus souvent sur les deux ; au contraire, sur les 25 *hardenbergi*, une seule nervure transverse a été trouvée, sur une aile antérieure. A l'aile postérieure de *cervina*, les nervures discocellulaires dessinent une ligne fortement brisée (fig. 13) ; dans l'autre espèce cette ligne tend vers la ligne droite (fig. 16).

Chez *cervina*, sclérites abdominaux (fig. 19), notamment ceux des urites 6, 7 et 8, nettement plus larges, proportionnellement à leur longueur, et pointes latéro-antérieures du 8e sternite relativement moins longues (mesures précises prises sur 6 préparations de *cervina* et 5 d'*hardenbergi*). Armure génitale bien plus grande (dimensions linéaires dans le rapport de 9 à 7). Partie repliée ventralement en gouttière du tegumen limitée par une ligne nettement brisée (fig. 21) ; chez *hardenbergi*, cette ligne est peu brisée ou ne l'est pas du tout (fig. 22). Maximum de largeur du vinculum situé un peu plus en arrière : rapport $\frac{l}{L}$ (fig. 21) valant 0,41 à 0,44, moyenne 0,425 sur les 6 préparations (*cervina*), contre 0,48 à 0,51, moyenne 0·495 sur 5 préparations (*hardenbergi*). Nombre de dents de l'extrémité distale du processus inférieur (sacculus) des valves plus élevé en moyenne (*cervina*, 4 à 9, moyenne 6,5 ; *hardenbergi*, 1 à 4, moyenne 2,5) ; processus supérieur (costa) formant une simple bosse à sa base, souvent remplacée chez *hardenbergi* (fig. 18) par un lobe distinct (4 exemplaires sur 5).

Femelle, premiers états et fourreaux de *cervina* sommairement décrits par Heylaerts (1888)—si la synonymie établie est exacte—et par Strand (1912). D'après le matériel étudié ici, la chrysalide et le fourreau mâles sont semblables, à la taille près, à ceux d'*hardenbergi*.

Comme on l'a vu, la forme *pictipennis* Strand se distingue à peine par un contraste plus accentué des parties colorées de l'aile antérieure du mâle.

Biologie très peu connue (Strand, 1912), probablement peu différente de celle d'*E. hardenbergi*. M. P. Rougeot, qui a élevé l'espèce au Gabon, et en a obtenu deux mâles, a trouvé les chenilles sur des arbres variés, notamment du genre *Citrus*, poussant dans la savane côtière ; ces larves ont été nourries de feuilles de *Citrus* et de Fromager ; cette espèce parait manquer dans la grande forêt. Les étiquettes du matériel étudié montrent que l'imago se trouve presque toute l'année, au moins de janvier à mars et de juin à novembre, mais ces dates varient probablement suivant les régions.

Espèce répandue en Afrique occidentale et équatoriale. Gambie : Captain Moloney, Joicey coll., lectotype de Druce (British Museum) ; *id.*, Joicey coll. (*id.*). Sierra Leone : Freetown, L. S. Lt. v. Raisp (Musée de Vienne). Gold Coast : Bibianaha, 70 miles N.W. of Dimkwa, 700 feet, 15.xi.09, H. G. F. Spurrell (British Museum). Cameroun : Efulen, 21.iii.22 au 10.xi.22, H. L. Weber, 10 ♂ (Carnegie Museum). Ile Fernando Po : Biapa (Concepcion), 1933, F. Bonet, J. Gil (Inst. d'Ent., Madrid). Guinée Espagnole : Alén, région de Benito, 15–30.vi.06, G. Tessmann, holotype et un paratype de *pictipennis* Strand (Musée de Berlin). Gabon : Oyem, P. Rougeot (Muséum de Paris) ; Mayumba, 3 et 17.i.52, P. Rougeot, 2 ♂ (*id.*). Congo Belge : Elisabethville, Katanga, 1934, Mlle. Kerkvoorde (Musée de Tervuren) ; *id.*, 4.x.49, don de S. G. Kiriakoff, 2 ♂ (Muséum de Paris) ; Flandria, Equateur, 13.ix.34, R. P. Hulstaert (Musée de Tervuren) ; Lulua, Tshala, vii.32, G. F. Overlaet (*id.*) ; Lulua, Kapanga, 6.viii.33 à iii.34, G. F. Overlaet, 6 ♂ (*id.*).

Le type de *moddermanni* Heylaerts (synonyme probable de *cervina*) provenait de Ho, Côte de l'Or.

Eumeta rougeoti sp. n. (Pl. 1, fig. 1 à 4.)

Je propose ce nom pour désigner notre espèce C, en la dédiant à M. P. Rougeot, Administrateur de la France d'Outre-Mer, qui, depuis plusieurs années, élève avec succès des Psychidae africains, et a obtenu le mâle de cette espèce.

Il s'agit ici, sans aucun doute, d'une espèce bien distincte des précédentes. Elle n'a jamais été citée dans la littérature entomologique, sauf peut-être sous forme de chenille ou de fourreau, mais cette possibilité semble actuellement invérifiable.

Cet *Eumeta* se reconnait assez facilement par l'aspect extérieur : forme, coloration et densité d'écaillement des quatre ailes.

Envergure 32 à 37 mm., le plus souvent 34 à 36 mm. (holotype 36 mm.) ; longeur de l'aile antérieure, de la base à l'apex, 14 à 17 mm.

Nombre d'articles antennaires : 32 à 42.

Les quatre ailes nettement plus foncées et plus opaques que chez les deux précédentes espèces, caractère du à une plus grande densité d'écaillement, et, en certains endroits de l'aile antérieure, à un plus grand nombre d'écailles larges et une proportion plus faible d'écailes blanches. Aile antérieure à parties blanches ou transparentes très réduites : chez les exemplaires frais, les taches translucides manquent, sauf celle de la région proximale de la cellule 7–8, d'ailleurs plus réduite que chez *hardenbergi* ; en particulier, les cellules 2–3 et 3–4, généralement translucides chez cette dernière espèce, sont ici de la teinte du fond, c'est-à-dire d'un brun opaque. Taches marginales blanches (parfois rougeâtre-clair), petites mais bien visibles dans les cellules 4–5 et 6–7. Le reste de l'aile est d'un brun opaque, d'intensité variable suivant les endroits, mais plus foncé, moins teinté de gris, que chez *cervina*, nettement brun-rouge, presque chocolat, au moins chez les exemplaires un peu anciens. Base de la cellule 5–6 généralement un peu moins sombre que celle de la cellule 6–7, alors que c'est souvent l'inverse chez les espèces précédentes. Nervures 1b, 2 à 8, discocellulaires et bord postérieur de la cellule discoïdale, plus fortement chargés de noir.

Aile postérieure d'un brun foncé uniforme (peut-être presque noir à l'éclosion), avec un ou deux points marginaux clairs plus ou moins visibles, souvent nuls.

Dessous des quatre ailes de teinte particulièrement sombre, pouvant présenter sur un exemplaire frais un reflet bleu-violet assez intense si on l'examine sous une lumière vive.

Forme des ailes caractéristique : par comparaison avec les deux espèces précédentes, les ailes antérieures sont plus courtes et proportionnellement plus larges, à bord externe moins oblique, et les postérieures sont plus arrondies au bord externe avec l'apex souvent moins net ; ces différences sont bien visibles sur la planche 1. Pour préciser, et en raison de la variabilité individuelle, ces caractères ont été exprimés par des nombres pour l'aile antérieure : les trois angles de l'aile n'étant pas des points définis, il est nécessaire de les remplacer par trois points A, B, C tels que ceux de la figure 15, A et C étant les extrémités distales des nervures 8 et 1b, B étant l'extrémité proximale de la nervure 1c ; sur la face dorsale de l'aile, B est également le point de la membrane alaire le plus proche de la base de l'aile, situé dans le creux limité par le cubitus et la branche antérieure de la fourche basilaire de 1b. Ce sont des considérations d'ordre pratique qui ont dicté ce choix ; les mesures peuvent être prises sur la face dorsale de l'aile. Le segment CD représente la distance minimum séparant la côte du point C. Voici le résultat des mesures prises au micromètre.

(*a*) Largeur relative de l'aile $\frac{C\ D}{A\ B}$

hardenbergi, 0,43 à 0,49 ; moyenne 0,45 (14 exemplaires)
cervina, 0,43 à 0,49 ; moyenne 0,45 (21 exemplaires)
rougeoti, 0,46 à 0,53 ; moyenne 0,50 (17 exemplaires)

(*b*) Obliquité du bord externe, exprimée par la valeur de l'angle ACB

hardenbergi, 109 à 117° ; moyenne 115°.
cervina, 107 à 119° ; moyenne 114°.
rougeoti, 99 à 111° ; moyenne 105°.

Ces nombres sont certainement significatifs, ayant une valeur statistique pour caractériser *rougeoti*, mais les moyennes indiquées ne sont là que comme indication, étant forcément arbitraires.

Nervulation d'*E. rougeoti* présentant par rapport aux deux autres espèces quelques différences. A l'aile antérieure, 7 assez souvent tigée avec 8 + 9 ; cellule discoïdale (fig. 14) relativement plus large, plus symétrique par rapport à son axe longitudinal : partie antérieure moins étirée vers l'apex, et branches de la media divisant cette cellule en trois parties ayant presque la même largeur (division au contraire très inégale chez *cervina*, fig. 13) ; branche postérieure de la media aboutissant assez loin de la tige 4 + 5, entre celle-ci et 6 (chez de nombreux *cervina*, cette branche aboutit très près de cette tige et parfois dans son prolongement) ; nervure transverse reliant 1c et 2 rarement présente (2 exemplaires seulement), mais 1c assez souvent développée un peu plus loin que la nervure la réunissant à 1b (5 exemplaires).

A l'aile postérieure, nervure transverse reliant 7 et 8 présente sur 6 exemplaires, et discocellulaires en ligne brisée à peu près comme chez *cervina*.

Sternites abdominaux en moyenne intermédiaires, quant à leur largeur relative, entre ceux des deux espèces précédentes, notamment le 8e sternite chez lequel la longueur relative des deux pointes antérieures est en outre sensiblement comme chez *hardenbergi* (6 préparations de *rougeoti*).

Armure génitale (8 préparations) à tegumen semblable à celui d'*hardenbergi* ; vinculum présentant un rapport $\frac{l}{L}$ (fig. 21) variant de 0,43 à 0,49 (moyenne 0,47) ; processus inférieur (sacculus) ayant 2 à 5 dents terminales (moyenne 3,5), et dépourvu du lobe (pulvillus) observé chez *hardenbergi*.

Les femelles qui ont été obtenues d'élevage n'ont pas été conservées.

Chenille inconnue.

Le seul fourreau appartenant avec certitude à cette espèce est un fourreau de mâle, mesurant 5 cm. de long sur 1 de diamètre ; semblable à ceux d'*hardenbergi*, il est recouvert de quelques fragments de tiges et d'une dizaine d'épines rectilignes longues de 3 à 5 cm.

M. P. Rougeot a découvert l'espèce à Oyem (Gabon) ; contrairement à *E. cervina*, *rougeoti* se trouve dans la zone de la grande forêt ; les fourreaux, peu abondants, se rencontrent sur des plantes variées, sur le tronc et les branches des arbres, notamment Oranger, Citronnier et Filao, souvent à 1,50m. ou 2m. au dessus du sol. Le mâle éclot dans la soirée et vole (en captivité) dès la tombée de la nuit ; un exemplaire a été attiré vers 23 h. par la lumière. La femelle obtenue, non fécondée, a fini par quitter son fourreau et a vécu ensuite encore une dizaine de jours.

M. P. Boutin a découvert les fourreaux à Port Gentil (Gabon), en pleine ville et aux environs ; une femelle, obtenue d'élevage, a attiré un mâle vers 6 h. du matin.

L'éclosion des imagos a lieu à différentes époques de l'année : mars, mai, août, septembre.

Espèce répandue en Afrique occidentale et équatoriale.

Holotype (♂) (Pl. 1, fig. 1) : GABON : Port Gentil, viii.49, P. Boutin (Muséum de Paris). Paratypes (19 ♂) : CÔTE D'IVOIRE : 1918, 2 ♂ Cremer (Muséum de Paris) ; CÔTE DE L'OR : Ajinah, G. C. Dudgeon (British Museum) ; Sekondi, Joicey coll. (*id.*) ; NIGERIA : Lagos, 5.v.10, J. A. de Gaye (*id.*) ; GABON : Oyem, P. Rougeot (Muséum de Paris) ; Lambaréné, Ogooué, R. Ellenberger, 2 ♂ (*id.*) ; N'Benguelila, env. de Tchibanga, 16.viii.52, P. Rougeot (*id.*) ; Kangwé, Ogooué, A. C. Good, 2 ♂ (Carnegie Museum) ; CONGO BELGE : A. Dumez (Muséum de Paris) ; Kadjudju, région du Lac Kivu, G. Babault 5 ♂ (*id.*) ; Ibanda, W. Kivu, Vandelannoite, 2 ♂ (Musée de Tervuren).

Citons également deux mâles de l'Ouroundi, 1800m., 27 et 28.ix.11, H. Meyer (Musée de Berlin), qui sont certainement des *rougeoti*, malgré quelques petites différences morphologiques.

Eumeta strandi sp. n. (Pl. 1, figs. 12 *b*, *c*.)

Deux exemplaires, dont l'un est un paratype de *pictipennis* Strand, n'ont pu être attribués à aucune des trois espèces précédentes ; ils concordent d'ailleurs entre eux de façon parfaite, tant par leur morphologie que par leur provenance—Guinée Espagnole et Gabon. Il ne parait pas possible d'y voir autre chose qu'une quatrième espèce.

Aspect général et taille voisins de ceux d'*hardenbergi*. Envergure 29 et 31 mm. 29 articles antennaires chez les deux exemplaires, nombre nettement inférieur à tous ceux comptés chez les autres espèces (32 à 43).

Coloration voisine de celle d'*E. rougeoti*, un peu moins foncée, mais plus que chez *hardenbergi* ; absence complète d'écailles blanches et de poils blancs, notamment sur le thorax et les ailes antérieures (à examiner sur fond noir), caractères séparant ces deux exemplaires des trois espèces précédentes. Ailes antérieures à nervures fortement marquées de noir, à cellule 2–3 bien écaillée, brune et opaque (claire et plus ou moins transparente chez *hardenbergi*), les seules régions transparentes étant la cellule 4–5, les deux tiers basilaires des cellules 3–4 et 7–8, et un point marginal situé dans la cellule 6–7. Ailes postérieures d'un brun presque aussi foncé que chez *rougeoti*.

Largeur relative $\frac{C\,D}{A\,B}$ (fig. 15) de l'aile antérieure et forme de l'aile postérieure à peu près comme chez *hardenbergi* ; angle ACB de l'aile antérieure valant respectivement 109 et 110°.

Cellule discoïdale de l'aile antérieure sensiblement comme chez *rougeoti*, c'est-à-dire relativement symétrique par rapport à son axe longitudinal.

Les deux armures génitales ont été préparées. Largeur relative des sternites abdominaux à peu près comme chez *cervina* donc plus grande que chez *hardenbergi*. Tegumen comme chez *hardenbergi* et *rougeoti* ; rapport $\frac{l}{L}$ du vinculum (fig. 21) égal à 0,49 et 0,50 ; nombre de dents terminales du processus inférieur variant de 2 à 4 (moyenne 2,5 sur les 4 valves).

Les caractères distinctifs de *E. strandi* les plus importants ou les plus frappants peuvent se résumer de la façon suivante.

(*a*) Par rapport à *hardenbergi* : coloration légèrement plus sombre, cellule 2–3 de l'aile antérieure foncée et opaque, aile postérieure plus foncée, cellule discoïdale de l'aile antérieure plus symétrique, sternites plus larges.

(*b*) Par rapport à *cervina* : taille plus faible, aile postérieure plus foncée, cellule discoïdale de l'aile antérieure plus symétrique, bords du tegumen, côté ventral, non brisés, rapport $\frac{l}{L}$ du vinculum plus grand, nombre de dents du processus inférieur bien plus petit.

(*c*) Par rapport à *rougeoti* : cellule 3–4 de l'aile antérieure transparente, bord externe plus oblique.

En outre, *E. strandi* diffère de ces trois espèces par un nombre moins élevé d'articles antennaires, et par l'absence complète d'écailles et poils blancs sur le thorax et les ailes antérieures. C'est de *rougeoti* que cette espèce se rapproche le plus, malgré sa ressemblance superficielle avec *hardenbergi*.

Femelle, premiers états et fourreau inconnus.

Holotype (♂), GABON : Ogooué, Lambaréné, R. Ellenberger (Muséum de Paris). Paratype (♂), GUINÉE ESPAGNOLE : Alén, Benitogebiet, 1–15.ix.06, G. Tessmann S.G. (paratype de *pictipennis* Strand) (Musée de Berlin).

VI. EXEMPLAIRES DE DÉTERMINATION INCERTAINE.

Parmi le matériel étudié, quelques exemplaires n'ont pu être déterminés avec certitude, soit à cause de leur mauvais état, soit à cause de leur nanisme (dû probablement aux conditions d'élevage) modifiant leur aspect, soit pour d'autres raisons.

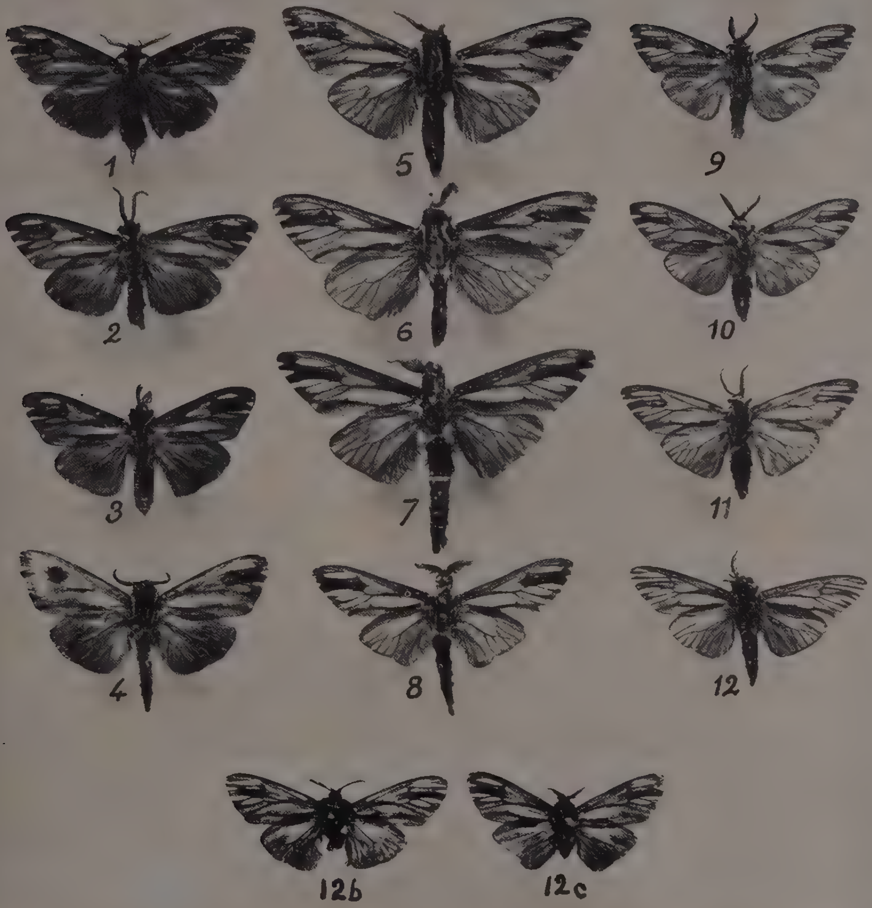
L'un d'eux mérite une mention spéciale ; il provient de la coll. Charles Oberthür (British Museum (Natural History)) et porte une grande étiquette (apparemment étiquette de commerçant) : " Eumeta Moddermanni Heyl.—Delagoa Bay ". Il n'appartient à aucune des espèces précédentes, présentant au contraire les caractères d'une espèce asiatique (notamment par l'armure génitale) ; il est probable qu'il s'agit d'une erreur d'étiquetage, et que cet exemplaire n'est pas africain.

VII. CONCLUSIONS.

L'étude qui précède comporte un remaniement complet du genre pour la faune africaine. Il est toujours regrettable d'avoir à apporter de telles modifications, notamment d'être obligé ici de faire disparaître le nom de *moddermanni* Heylaerts, qui a été plusieurs fois cité et qui figure dans un certain nombre de collections ; mais ces changements sont indispensables si on veut voir cesser la grande confusion qui régnait dans ce petit groupe africain.

Le présent travail ne repose malheureusement, par nécessité, que sur la morphologie des mâles, et il faut souhaiter qu'on arrive une fois à connaitre et à comparer les femelles et les premiers états, ainsi que la biologie. Il est d'autre part très probable que l'on découvrira d'autres espèces, car ce qu'on sait actuellement des Psychides africaines est infime à côté de ce qui existe apparemment.

Pour le matériel qui m'a été aimablement communiqué par différents musées, je tiens à exprimer toute ma reconnaissance à MM. R. Agenjo (Madrid), L. Berger (Tervuren), le Dr. H. K. Clench (Pittsburgh), les Professeurs M. Hering (Berlin) et B. Pittioni (Vienne), le Dr. C. O. van Regteren Altena (Leyde), Mr. N. D. Riley (Londres), le Professeur W. Roepke (Leyde), Mr. W. H. T. Tams (Londres), le Dr. J. A. Whellan (Salisbury), sans oublier le regretté Dr. W. R. Sweadner (Pittsburgh). Mes vifs remerciements sont dus également à tous ceux qui m'ont aidé sous diverses formes : MM. P. Boutin, A. Dufrane, N. Hallé, F. M. Jones, S. G. Kiriakoff, le Dr. E. Lindner, R. Mouterde, P. Rougeot et P. Viette.

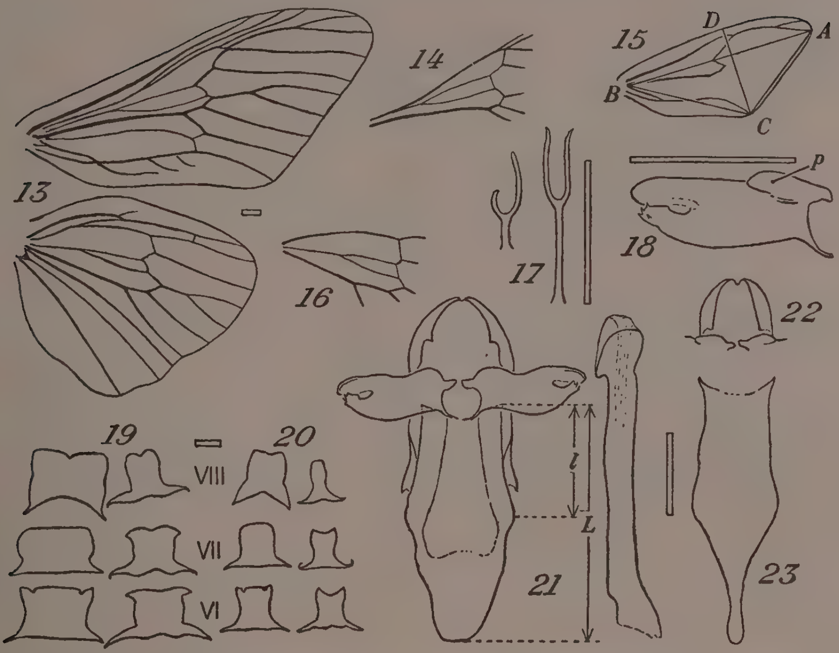


Espèces africaines du genre *Eumeta*.

Figs. 1 à 4, *Eumeta rougeoti* sp. n. (1) holotype, Port Gentil, Gabon. (2) à (4) paratypes. (2) et (3) Kangwé, Ogooué, Gabon. (4) N'Benguelila, env. de Mayumba, Gabon. Figs. 5 et 6, *Eumeta cervina* Druce. (5) Elisabethville, Congo Belge. (6) Lulua, Kapanga, Congo Belge. Figs. 7 et 8, *E. cervina* f. *pictipennis* Strand, Alén, Guinée Espagnole. (7) holotype. (8) paratype. Figs. 9 à 12, *Eumeta hardenbergi* sp. n. (9) holotype, Baie Delagoa. (10) à (12) paratypes. (10) Baie Delagoa. (11) Mozambique. (12) Natal. Figs. 12*b–c*. *Eumeta strandi* sp. n. (*b*) holotype, Ogooué, Lambaréné, Gabon. (*c*) paratype, Alén, Guinée Espagnole.

Tous ces exemplaires reproduits en grandeur naturelle.

J. Bourgogne. *Adlard & Son, Ltd., Dorking*



Figs. 13–23. (13) nervulation d'*Eumeta cervina*. (14) cellule discoïdale, aile antérieure, d'*E. rougeoti*, à la même échelle. (15) mensuration de l'aile antérieure. (16) cellule discoïdale, aile postérieure, d'*E. hardenbergi* ; même grossissement que (13) et (14). (17) deux types de pectinations ramifiées ; l'une, de la base du flagelle chez *cervina* (à gauche), l'autre, du 13e article antennaire chez *hardenbergi* (à droite). (18) valve gauche, face ventrale, d'*E. hardenbergi* ; *p*, pulvillus. (19) sclérites des urites 6 à 8 d'*E. cervina* ; sternites à gauche, tergites à droite. (20) id. chez *E. hardenbergi*, à la même échelle. (21) à (23) armures génitales, les trois figures à la même échelle. (21) *E. cervina*, le pénis vu de profil. (22) partie postérieure du tegumen d'*E. hardenbergi*. (23) vinculum d'un *Eumeta* asiatique indéterminé (Manille, Philippines).

Le double trait placé à côté de certaines figures (13, 17, 18, 19–20, 21–23) représente 1 mm.

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NEOTROPICAL MOTHS OF THE GENUS *ORTHOCOMOTIS* DOGNIN (LEPIDOPTERA : TORTRICIDAE).

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With 6 Line Plates.

For many years the tortricid moth species referred to below have been placed in the genus *Eulia* Hübner. Although such authors as Dognin[1] and Busck[2] recognized the differences between these moths and *ministrana* (L.), the type of *Eulia*, their opinions were disregarded and these species, and many more unrelated forms, were placed in the " waste basket " *Eulia*. From my studies of the material reported on here it appears clear that *Orthocomotis* is Neotropical and further collections will show that it is a much larger genus than indicated by the present paper.

Dognin placed only one species, *olivata*, in his genus *Orthocomotis* but Busck, when he proposed *Sociphora*, a synonym of *Orthocomotis*, recognised that not only the type species of *Sociphora*, *Penthina magicana* Zeller, was distinct but that the genus included also *Penthina muscosana* Zeller, and a new species, *S. herbaria* Busck, belonged together.

In the present paper I include twelve previously described species and describe seventeen more in *Orthocomotis*.

In habitus all but two, *scardiana* (Dognin) and *smaragdophaea* (Meyrick), fall into an apparently natural pattern. The two mentioned are placed here with reservations and may require new genera. The male genitalia show a division into two groups within the genus, but the female genitalia do not show any such sharp division. The hind wing also indicates a natural division within the genus by the roughened condition in the four species *herbacea*, *nitida*, *leucothorax* and *melania*, but this division is not supported by any other characters and must be considered as only specific. Two species, *cristata* and *melania* possess a *cubital pecten*, a startling character for a tortricid! Otherwise the moths present a most homogeneous appearance.

This paper is based primarily on material in the U.S. National Museum, but I am greatly indebted to Dr. Hans Strouhal, Director, Naturhistorisches Museum, Vienna, for the loan of the type of *Eulia melanochlora* Meyrick and other specimens associated with it. I am also indebted to Mr. John D. Bradley, British Museum (Natural History), for the drawing of the male genitalia of *Penthina muscosana* Zeller. The remaining drawings for this paper were made by Arthur D. Cushman, Entomology Research Branch, United States Department of Agriculture.

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[1] Dognin, Paul, 1905, *Ann. Soc. ent. Belg.* **49** : 85.

[2] Busck, A., 1920, *Insec. Inscit. menst.* **8** : 85.

Orthocomotis Dognin.

Orthocomotis Dognin, 1905, *Ann. Soc. ent. Belg.* **49** : 85. (Type species : *Orthocomotis olivata* Dognin, *ibid.* [by monotypy and original designation]).
Sociphora Busck, 1920, *Insec. Inscit. menst.* **8** : 85. (Type species : *Penthina* (*Sericoris*) *magicana* Zeller, 1866, *Stettin. ent. Ztg.* **27** : 150, pl. 1, fig. 9 [by original designation]).

This genus may be distinguished from *Eulia* Hübner, 1826, with which it has been confused by Meyrick, by the much longer third segment of palpus, the rough, coarse scaling of the head, veins 3 and 4 of fore wing approximate, and the almost complete absence of discocellulars in the hind wing.

All the species of *Orthocomotis* that are known are Neotropical ; *Eulia* is holarctic, confined to the more northern areas of that region.

Key to the species of *Orthocomotis* Dognin.

1. Hind wing underside mottled 5
Hind wing underside not mottled 2
2. Hind wing with cubital pecten 3
Hind wing without cubital pecten 4
3. Surface of hind wing roughened by upturned scales . . . **melania** sp. n.
Surface of hind wing smooth . . . . . . **cristata** sp. n.
4. Surface of hind wing roughened by upturned scales ; fore wing with yellowish hue . . . . . . **nitida** sp. n.
Surface of hind wing not roughened ; fore wing without yellowish hue **herbaria** (Busck)
5. Ground colour of fore wing green 6
Ground colour of fore wing not green 7
6. Frons pale greenish . . . . . . **mareda** sp. n.
Frons fuscous . . . . . . **melanochlora** (Meyrick)
7. Ground colour of fore wing vinaceous-lilac . . . . . . **jordani** sp. n.
Ground colour of fore wing otherwise 8
8. Fore wing with conspicuous ochreous or ochreous-orange spots in terminal half 9
Fore wing without such spots 14
9. Alar expanse under 23 mm. . . . . . . **ochrosaphes** sp. n.
Alar expanse over 24 mm. 10
10. Fore wing with conspicuous white apical spot 11
Fore wing without such spot 12
11. Fore wing predominantly whitish . . . . . . **boscantina** (Dognin)
Fore wing not predominantly whitish . . . . . . **euchaldera** sp. n.
12. Dark preapical blotch conspicuous, and extending to vein 3 . . . 13
Dark preapical blotch not conspicuous and not extending to vein 3 **ochracea** sp. n.
13. Fore wing with brassy hue . . . . . . **olivata** Dognin
Fore wing without brassy hue . . . . . . **exolivata** sp. n.
14. Thorax predominantly white or whitish 15
Thorax otherwise 18
15. Upper surface of hind wing smooth 16
Upper surface of hind wing roughened . . . . **leucothorax** sp. n.
16. Frons white . . . . . . **magicana** (Zeller)
Frons otherwise 17
17. Fore wing mostly blackish with contrasting white markings on dorsum **argodonta** sp. n.

Fore wing mottled without contrasting white markings on dorsum **smaragditis** (Meyrick)
18. Fore wing with slender, light coloured, oblique mark from costa, near apex, to outer end of cell 19
Fore wing without such mark 20
19. Alar expanse over 35 mm. . . . . **scardiana** (Dognin)
Alar expanse under 25 mm. . . . . **citroleuca** (Meyrick)
20. Fore wing with at least two transverse fasciae from costa to dorsum or tornus . . . . **smaragdophaea** (Meyrick)
Fore wing without such fasciae 21
21. Apex of fore wing with conspicuous white patch 22
Apex of fore wing without such white patch 23
22. Termen of fore wing with four green spots . . . . **prochaldera** sp. n.
Termen of fore wing with six green spots . . . . . **chaldera** (Druce)
23. Hind wing upper surface roughened . . . . . . **herbacea** sp. n.
Hind wing upper surface not roughened 24
24. Dark markings of fore wing well-defined, contrasting 25
Dark markings of fore wing obscured, mottled 27
25. Ground colour of fore wing buff, suffused with light greyish-fuscous **pseudolivata** sp. n.
Ground colour of fore wing otherwise 26
26. Pale markings of fore wing forming a coarse reticulum **muscosana** (Zeller)
Pale markings of fore wing not forming a reticulum . **subolivata** sp. n.
27. Dark areas of fore wing mouse-grey and blackish . . . . . **aglaia** sp. n.
Dark markings of fore wing greyish-fuscous, partly overlaid with chocolate . . . . **twila** sp. n.

Orthocomotis melanochlora (Meyrick) **comb. nov.**

(Pl. I, figs. 1–1*a* ; Pl. V, fig. 3.)

Eulia melanochlora Meyrick, 1931, *Exotic Microlepidoptera* 4 (5) : 151.

Male genitalia.—See figures (Slide No. 10326).
Female genitalia.—As figured (Slide No. 10327).

Type.—In the Naturhistorisches Museum, Vienna.

Type locality.—BRAZIL : Minas Geraës, Passo Quatro, 1921–22 (*Zikan*).

Remarks.—The type bears a small white label with "*Eulia melanochlora* n. sp.", in Meyrick's hand, on the bottom of which is printed "det. Meyrick". Meyrick described *melanochlora* from 13 specimens, but his series was mixed. With the type I associate two males and three females, all from BRAZIL, as follows : Minas Geraës, Passo Quatro, 1921–22, ♀ (*Zikan*) ; Nova Teutonia, ii. 1948, 2 ♀ (*Fritz Plaumann*) ; São Paulo, 2 ♂ (*R. Spitz*).

The other specimens listed by Meyrick, together with additional material, represent another species described below.

The two female specimens from Nova Teutonia have somewhat atypical genitalia but I think represent only a variety. In all other details they agree with the type.

Orthocomotis mareda sp. n.

(Pl. I, figs. 3–3*b* ; Pl. V, fig 4.)

Alar expanse 21–28 mm.

Labial palpus ochreous-white ; second segment wholly suffused with blackish-fuscous externally except tip, and suffused with blackish-fuscous inwardly on basal half ; apical segment suffused blackish-fuscous except base and apex. Antenna fuscous except scape, which is celandine green narrowly edged ochreous-white apically. Head with face celandine green and vertex ochreous-buff, the tips of the scales lightly infuscated. Thorax and forewing celandine green ; tegula and thoracic tuft fuscous-tipped ; costa narrowly edged with white and scattered along costa several blackish spots ; from basal fifth of costa a black crescentic fascia extends approximately to centre of wing, turns abruptly and terminates in a broad pretornal blotch ; at the angle of the crescentic fascia and pretornal blotch is a patch of pale brownish scales followed by scattered yellowish and malachite green scales ; before termen an irregular blackish spot ; inner margin of wing edged with a series of small black spots ; cilia blackish in middle of termen, whitish at apex and tornus. Hind wing fuscous, strongly mottled with whitish beneath ; cilia fuscous with a fine, light basal line. Legs ochreous-white banded and suffused with fuscous. Abdomen fuscous above, ochreous-white beneath with a longitudinal, ventral line of black spots.

Male genitalia.—See figures (Slide No. 10276).

Female genitalia.—As figured (Slide. 10282).

Type.—U. S. N. M. No. 62736.

Type locality.—Brazil : Nova Teutonia.

Remarks.—Described from the ♂ type, 5 ♂ and 16 ♀ paratypes as follows : Brazil : Nova Teutonia, 3 ♂, ♀, v.1938 (*Fritz Plaumann*) ; São Paulo, Alto da Serra, ♂, 29–30.x.27 (*Zerny*), São Paulo, Tayó, S.C., ♀, 16.viii (*B. Pohl*, No. 128) ; New Bremen, ♀, ix.1936 (*Fritz Hoffmann*) ; Santa Catharina, 2 ♂, 14 ♀, July and September dates, 1935, 1936 (*Fritz Hoffmann*). Paratypes in the U.S. National Museum, British Museum (Natural History) and the Naturhistorisches Museum, Vienna.

This is the species Meyrick had mixed with typical *melanochlora*. It is not only easily distinguished from *melanochlora* by the genitalia (compare figures) but is immediately separable on the colour of the head and face which are ochreous-buff and celandine green respectively in *mareda* and both fuscous in *melanochlora*. Although both possess a dark pretornal blotch, or spot, on the fore wing this is never confluent with the crescentic fascia in *melanochlora*, but is always connected with the fascia in *mareda*.

Orthocomotis jordani sp. n.

(Pl. I, figs. 5–5*a*).

Alar expanse 22 mm.

Labial palpus ochreous-white ; second segment overlaid with fuscous outwardly, except tip, and inwardly, except distal third ; third segment with some fuscous scaling outwardly and above. Antenna, except scape, fuscous ; scape ochreous-white with faint pearl-grey above. Head ochreous-white, scales of vertex more buff. Thorax and fore wing light vinaceous-lilac ; dorso-anteriorly thorax faint pearl-grey, tegula and posterior tuft fuscous tipped ; costa of fore wing narrowly edged whitish with large and small blackish markings and spots ; from basal fifth of costa an irregular, oblique blackish fascia extends to about centre of cell ; beyond this a large quadrate blackish costal spot below which is another smaller one of the same colour ; pre-apical costal spot triangular, blackish ;

base of wing, basal angle and a series of small dorsal spots, blackish; pre-tornal blotch, extending to centre of wing at end of cell and a pre-terminal subtriangular spot, blackish; spots and blotches and pre-terminal area of wing with scattered yellowish and green scales; cilia blackish along termen, at apex and tornus ochreous-white. Hind wing light fuscous, underside mottled with ochreous-white; cilia concolorous, except lighter at extremities and with pale basal line. Legs ochreous-white variously banded and suffused with blackish. Abdomen ochreous-white; hair-like scales (dorsal) greyish-fuscous; anal tuft irrorate with fuscous; beneath irrorate and suffused with blackish-fuscous.

Male genitalia.—See figures (Slide No. 1030).

Female genitalia.—Unknown.

Type.—U. S. N. M. No. 62737.

Type locality.—BRAZIL: New Bremen.

Remarks.—Described from the unique type (11.viii.36. *Fritz Hoffmann*).

In pattern and genitalia strikingly similar to *mareda* but immediately distinguished from that species by the vinaceous colour of the fore wing and the absence of the basal pad of the harpe. The lateral processes of the transtilla are less divergent and the anellus is narrower.

It gives me great pleasure to dedicate this species to Dr. Karl Jordan who has for so many years distinguished himself in the field of entomology.

Orthocomotis nitida sp. n.

(Pl. IV, fig. 2.)

Alar expanse, 21 mm.

Labial palpus ochreous-white, almost wholly suffused with greyish-fucous. Antenna greyish-fuscous; scape ochreous-white beneath and with a red-brown spot near base above; shaft with some red-brown scaling near base above. Head ochreous-white with purplish-fuscous between antennae and frons red-brown. Thorax and ground colour of forewing ochreous-white with prothorax fuscous; remainder mixed red-brown, yellowish and green scales; dark markings of forewing fuscous, in part overlaid with red-brown, the latter colour outlining the veins; the fuscous markings are as follows: on costa at base, basal fifth, middle and preapically large blotches, the preapical one extending to vein 2 near termen; base of wing and pretornal spot extending beyond fold; pale, shining green scales along fold, along costal area and in apical third of wing; light areas of wing with distinct yellow hue; cilia yellowish with scattered fuscous and red-brown scales. Hind wing greyish-fuscous; cilia concolorous with a light basal line; the scales of upper surface slightly upturned giving a roughened appearance and with slight greenish iridescence between scale-ridges thus formed; underside unmottled. Legs ochreous-white suffused and banded with greyish-fuscous and red-brown.

Male genitalia.—See figure. (Slide No. AB, 20 September, 1932.)

Female genitalia.—Unknown.

Type.—U. S. N. M. No. 62743.

Type locality.—GUATEMALA: Cayuga.

Remarks.—Described from the ♂ type, dated "4" collected by *Schaus* and *Barnes*.

This species is nearest *herbaria*, but differs from it by the yellowish hue of fore wing and roughened scales of hind wing. The harpe of *nitida* is also much narrower and more triangular.

Orthocomotis herbaria (Busck) **comb. nov.**

(Pl. III, figs. 4–4*a* ; Pl. IV, fig. 1.)

Sociphora herbaria Busck, 1920, *Insec. Inscit. menst.* **8** : 85.

Male genitalia.—See figures (Slide No. AB, 18 February, 1920).
Female genitalia.—As figured (Slide No. 10298).

Type.—In the United States National Museum.

Type locality.—GUATEMALA : Cayuga.

Remarks.—With the type I associate one male and three females from GUATEMALA as follows : Cayuga, 2 ♀ (" 4/18 ") ; Tuis, 2400 ft., ♀ (no date) ; Purulha, ♂ (no date). All were collected by *Schaus* and *Barnes*.

Orthocomotis chloantha (Walsingham) **comb. nov.**

Tortrix chloantha Walsingham, 1914, *Biologia Centrali-Americana, Lepidoptera-Heterocera* **4** : 278.

Eulia chloantha (Walsingham), Meyrick, 1926, *Exotic Microlepidoptera* **3** (8) : 249.

Type.—In the British Museum (Natural History).

Type locality.—MEXICO : Sierra de las Aguas Escondidas, 7000 ft., Guerro.

Remarks.—The species obviously belongs here and from the description most closely resembles *chaldera*.

Orthocomotis ochracea sp. n.

(Pl. II, figs. 4–4*a*.)

Alar expanse, 27 mm.

Labial palpus ochreous-white ; second segment infuscated exteriorly ; third segment with median greyish-fuscous annulus. Antenna greyish-fuscous ; base of shaft and upper surface of scape with some chocolate scaling ; scape ochreous-white beneath. Head dark tawny with white mixed laterally ; below antennae chocolate ; face white. Thorax greyish-fuscous ; prothorax and base of tegula chocolate ; some yellowish-green scales at base of tegula. Forewing ground colour ochreous-white ; dark markings poorly defined, fuscous, as follows : an outwardly oblique fascia from basal fifth of costa to fold and outward to middle of cell ; a blotch from mid-costa to end of cell ; a broad preapical spot ; a broad pretornal blotch extending to end of cell ; between the costal markings, in terminal area, in and beyond cell and at base and along dorsum some lines or spots of white scales ; across wing, from about middle of costa to tornus, and along dorsum some spots of ochreous-orange scales ; malachite green patches of scales along fold, basal third of costa, in and beyond cell and a spot at apical third well inside costa. Hind wing greyish-fuscous ; cilia concolorous with pale basal line ; underside mottled with ochreous-white. Legs ochreous-white suffused and banded with greyish-fuscous. Abdomen greyish-fuscous above, ochreous-white beneath with three longitudinal lines of greyish-fuscous spots.

Male genitalia.—See figures (Slide No. 10435).
Female genitalia.—Unknown.

Type.—U. S. N. M. No. 62752.

Type locality.—COSTA RICA : Juan Vinas.

Remarks.—Described from the ♂ type (no date, *Wm. Schaus*).

The general appearance of *ochracea* is similar to that of *twila*, but the latter is a smaller moth and lacks the ochreous-orange spots of the forewing.

The male genitalia of *ochracea* and *chaldera* are almost indistinguishable, the differences being qualitative rather than quantitative. The size, pattern and colouring easily distinguish the two and *chaldera* completely lacks the ochreous-orange spots of *ochracea*.

Orthocomotis chaldera (Druce) **comb. nov.**

(Pl. II, figs. 1–1*b* ; Pl. VI, fig. 3.)

Grammophora chaldera Druce, 1889, *Biologia Centrali-Americana, Lepidoptera-Heterocera* **1** : 259, pl. 26, fig. 5.
Tortrix chaldera (Druce), Walsingham, 1914, *Biologia Centrali-Americana, Lepidoptera-Heterocera* **4** : 278.
Eulia chaldera (Druce), Meyrick, *in* Wagner, 1912, *Lepidopterorum Catalogus* : 38 ; *in* Wytsman, 1913, *Genera Insectorum*, fasc. 149 : 38 ; 1926, *Exotic Microlepidoptera* **3** (8) : 249.

Male genitalia.—See figures (Slide No. 10427).
Female genitalia.—As figured (Slide No. 10437).

Type.—Lost ? [Not in British Museum (Natural History)].
Type locality.—Costa Rica : Volcan de Irazu, 6000 ft.
Remarks.—Mr. John D. Bradley has informed me that the type is not in the British Museum (Nat. Hist.), and I did not see it when I was there, but Druce's figure is so clear and the locality is so exact I do not hesitate to recognise the species.

Under this name I place three males and one female, all from Costa Rica, as follows : 2 ♂, Mount Poas ; ♀ Sixola River ; ♀, Juan Vinas. All were collected by *Wm. Schaus*, but no dates are recorded. With the above I associate with some misgiving, a female from Mexico : Misantla (14.x. (*R. Muller*, No. 4360)). Superficially this specimen matches exactly the other four, but is larger and the genitalia do not quite match those of the other female.

Previously these specimens stood under the name of *muscosana*, but are easily separated on genitalia and pattern.

Orthocomotis prochaldera sp. n.

(Pl. IV, fig. 3.)

Alar expanse, 37 mm.

Labial palpus greyish-fuscous except that inwardly second segment is ochreous-white. Antenna greyish-fuscous ; scape ochreous-white beneath. Thorax (rubbed) fuscous anteriorly mixed with chocolate. Forewing ground colour almost wholly overlaid with greyish-fuscous dark markings, as follows : from basal fifth a broad fascia to fold thence curved to near end of cell ; a broad blotch on costa about middle and another at apical fourth ; a large pretornal blotch and a smaller, oblique, rectangular spot from vein 2 to vein 6 ; basal fifth of dorsum ; at basal third and apical third irregular white bars, the first extending to middle of cell, the second to vein 9 near upper angle of cell ; these two bars overlaid with chocolate and yellow-green scales ; terminal fifth of wing white interrupted by the rectangular greyish-fuscous spot between veins 2 and 6 and yellowish-green spots along middle of termen ; on dorsum three irregular white spots ; at end of cell a large chocolate and yellowish-green spot partly infringing on the preterminal white area ; considerable chocolate and yellowish-green scaling irregularly over surface of wing ; cilia greyish-fuscous mixed with ochreous-white. Hind wing greyish-fuscous except whitish costal area ; cilia concolorous, paler-tipped and with a pale basal line ; underside mottled with ochreous-white. Legs, ochreous-white banded and suffused with greyish-fuscous.

Male genitalia.—Unknown.
Female genitalia.—As figured (Slide No. 10293).

Type.—U. S. N. M. No. 62749.
Type locality.—ECUADOR: Environs de Loja.
Remarks.—Described from the ♀ type (no date or collector indicated).

This species is similar to *chaldera*, but distinguished from it by its larger size, extensive white terminal area and the female genitalia. It is also similar to *euchaldera*, but lacks the rufous scaling of that species.

Orthocomotis euchaldera sp. n.

(Pl. IV, figs. 5–5*a*.)

Alar expanse, 30–32 mm.

Labial palpus ochreous-white; second segment strongly overlaid with greyish-fuscous except basal two-thirds inwardly and apex; second segment wholly infuscated except tip and a narrow white ring at base. Antenna greyish-fuscous except for russet scaling above on base of shaft, and a spot on upper surface of scape; scape white beneath. Head greyish-fuscous with russet and rufous scaling above, russet below antennae and a whitish face. Thorax greyish-fuscous; prothorax, base and apex of tegula and posterior tuft mixed with russet and rufous scales; tuft also with some white mixed; dark markings mostly fuscous, with mouse grey between. Forewing with dark markings as follows: an irregular, oblique, broad fascia beginning at basal fifth, extends to fold and end of cell; in fold it is confluent with a curved bar, the latter from near base of wing extending almost to tornus; on dorsum, within the arc of the curved bar, a large spot; from slightly beyond end of cell a large triangular spot extends to vein 2 and to apex, mostly confined inside termen; in the middle of this triangle is an elongate white spot extending to apex and containing three, small, irregular greenish-yellow spots; at base of wing, basal third of costa and on costa slightly beyond middle irregular white scaling; similar areas of white near base, in fold, and near centre of wing; greenish-yellow scaling inside costa to near middle, in cell and beyond end of cell and along fold; over entire wing, particularly along veins and in tornal area, rufous spots and short dashes. Hind wing greyish-fuscous; cilia concolorous, some tipped whitish, and with a pale basal line; underside mottled with ochreous-white. Legs ochreous-white banded and suffused with greyish-fuscous; foretibia and tarsi overlaid with russet. Abdomen light greyish-fuscous above, ochreous-white beneath strongly suffused with fuscous.

Male genitalia.—See figure (Slide No. 10292).
Female genitalia.—Unknown.

Type.—U. S. N. M. No. 62748.
Type locality.—COLOMBIA: San Antonio.
Remarks.—Described from the ♂ type, vi.09. (*Fassel*) and 3 ♂ paratypes from COLOMBIA as follows: ♂, Alto de los Ances, 2.x.08; ♂ San Antonio, Cali, without date; and ♂, "Colombia". All were collected by *Fassel*. Presumably the three paratypes are from the same place as the type, and taken at the same time, but only the type is dated. Paratypes in the U.S. National Museum and the British Museum (Natural History).

This species has been associated with *chaldera* and also *muscosana*. From both of these species *euchaldera* can be separated by the rufous scaling of the forewing.

Orthocomotis olivata Dognin.

(Pl. IV, figs. 4–4*a* ; Pl. V, fig. 5.)

Orthocomotis olivata Dognin, 1905, *Ann. Soc. ent. Belg.* **49** : 85.

Male genitalia.—See figures (Slide No. AB, April 1, 1926).
Female genitalia.—As figured (Slide No. 10296).

Type.—In the U.S. National Museum.
Type locality.—COLOMBIA : Popayan.
Remarks.—With the type I associate two males from Colombia. One is labelled " St. Antonio, Nov. 08 " and the other " Colombia, Fassel ". The latter also bears a label, in Durrant's handwriting, " *Tortrix* (*Eulia*) *chaldera* Druce, teste Drnt. 6549 ".

Two species from Brazil, described below, have been mixed with *olivata*, but *olivata* is at once distinguished from them by the pronounced brassy hue of the forewing.

Orthocomotis pseudolivata sp. n.

(Pl. III, figs. 3–3*a* ; Pl. VI, fig. 2.)

Alar expanse, 20–26 mm.

Labial palpus buff ; second segment suffused with light greyish-fuscous outwardly except at extreme base and apex ; third segment similarly suffused except at apex. Antenna, except scape, greyish-fuscous ; scape buff suffused with light greyish-fuscous and with a conspicuous chocolate brown spot in centre, above. Head buff suffused with light greyish-fuscous ; frons with chocolate brown spot on each side. Thorax and fore wing buff suffused over most of surface with light greyish-fucous ; prothorax, each side of mesothorax and base of tegula chocolate-brown more or less overlaid with shining emerald green scales ; costa narrowly edged ochreous-white and with a series of greyish-fuscous spots from base to apex ; blackish-fuscous markings as follows : base of wing, a crescentic fascia from basal fifth of costa to centre of cell ; a lunate spot at centre of costa and a similar one preapically with an oblique dash below to near centre of termen followed by four or five small spots grouped along termen ; a triangular spot between the crescentic fascia and preterminal dash ; a rectangular pretornal bar ; the crescentic costal fascia with slender extension from near costa nearly to fold and a similar curved one from outer third curved back into fold ; all above markings edged or variously overlaid with shining emerald green scales ; cilia ochreous-white marked with greyish-fuscous ; a few small, indistinct light greyish-fuscous spots along dorsum. Hind wing greyish-fuscous except buff along costa and mottled ochreous-white beneath ; cilia ochreous-white with a few greyish-fuscous spots and a greyish-fuscous subterminal line. Legs buff, spotted with chocolate-brown and fuscous. Abdomen light greyish-fuscous above, buff beneath with median ventral line of fuscous spots.

Male genitalia.—See figures (Slide No. 10288).
Female genitalia.—As figured (Slide No. 10290).

Type.—U. S. N. M. No. 62738.
Type locality.—BRAZIL : New Bremen.
Remarks.—Described from the ♂ type, 4 ♂ and 10 ♀ paratypes as follows : BRAZIL : New Bremen, 2 ♂, 5 ♀, 8.vii to 4.xii.1936 (*Fritz Hoffmann*) ; Rio de Janeiro, ♀, 27.iv.30 (*J. F. Zikan*, No. 253) ; Santa Catharina, 2 ♂, 4 ♀, 2.vi to 29.xi, 1935–36 (*Fritz Hoffmann*). Paratypes in the U.S. National Museum,

British Museum (Natural History) and the Naturhistorisches Museum, Vienna.

At first glance similar to *olivata* and previously confused and mixed with it. The complete absence from *pseudolivata* of any brassy sheen immediately distinguishes it from *olivata*. A comparison of the figures of the genitalia of the two species provides ample characters for the separation of the two species.

Orthocomotis exolivata sp. n.

(Pl. VI, fig. 4.)

Alar expanse, 25–27 mm.

Labial palpus buff; second segment overlaid with fuscous outwardly except apex and inwardly in apical half; third segment with fuscous spot in middle outwardly. Antenna, except scape, greyish-fuscous; scape buff overlaid above with reddish-brown. Head buff suffused with fuscous and face with reddish-brown patch above. Thorax and ground colour of forewing pale ochreous-white; ground colour of thorax obscured by brown suffusion; prothorax and base of tegula reddish-brown with mixed emerald green scaling; costal markings fuscous and heavy, many spots confluent; heavy fuscous markings as follows: from basal fifth a broad crescentic fascia extends to fold, thence to upper margin of cell opposite middle of costa where it merges with a costal spot; at apical fourth a broad, oblique blotch extends to vein 3; a large pretornal blotch extends from dorsum to near base of vein 7; along termen an elongate, narrow dash; all dark markings more or less overlaid with emerald scales but the emerald scales more pronounced along fold, from base of wing, beyond end of cell and in subterminal area; middle three-fifths of wing spotted with ochreous-orange; in tornus, and in costal half of wing, some dull leaden suffusion; cilia ochreous-white strongly marked with fuscous. Hind wing greyish-fuscous except whitish costa; underside mottled with ochreous-white. Legs buff suffused and banded with fuscous. Abdomen greyish-fuscous above, ochreous-white beneath irrorate with fuscous and with a pronounced median ventral line of fuscous spots.

Female genitalia.—See figure (Slide No. 10297).

Type.—U. S. N. M. No. 62739.

Type locality.—Brazil: Nova Teutonia.

Remarks.—Described from the ♀ type and 5 ♀ paratypes as follows: Brazil: Nova Teutonia, 3 ♀, viii.1936 (*H. J. Parish*; *Fritz Plaumann*); New Bremen, ♀, 2.ix.36 (*Fritz Hoffmann*); Rio de Janiero, ♀, 20.xi.29 (*J. F. Zikan*, No. 302). Paratypes in the U.S. National Museum, British Museum (Natural History) and the Naturhistorisches Museum, Vienna.

Very similar to *pseudolivata* but ground colour of forewing paler (nearly white) dark markings heavier but less rich in tone, and the light areas in middle three-fifths of wing spotted with ochreous-orange scales.

From *olivata* this species is distinguished by the absence of the brassy sheen and from both *olivata* and *pseudolivata* by the remarkable development of the ostium.

Orthocomotis subolivata sp. n.

(Pl. III, fig. 2.)

Alar expanse, 24 mm.

Labial palpus ochreous-white, suffused and overlaid with greyish-fuscous, especially outwardly; apices of both second and third segments ochreous-white. Antenna greyish-fuscous, except underside of scape, which is ochreous-white. Head cinnamon-buff above, dark brown below antennae; face ochreous-white. Thorax and ground colour of fore wing ochreous-white, the former suffused with greyish-fuscous; prothorax and base of tegula dark brown; apex of tegula and posterior tuft cinnamon-buff with fuscous mixed; dark markings of forewing fuscous, as follows: a series of small spots along costa; base of wing; at basal fifth a broad fascia extending to fold thence to centre of cell almost merging with a large blotch at middle of costa; from costa, before apex, a very broad blotch extends to vein 3, with a deep indentation of ground colour between veins 6 and 7; from vein 1b a narrow transverse triangular fascia extends across end of cell; along fold an elongate bar of red-brown, green and ochreous scales extends almost to tornus; dark markings overlaid with red-brown, green and ochreous scales and spots of the same mixed scales along dorsum, before termen, in and before end of cell, and along veins; cilia ochreous white mixed with greyish-fuscous and yellowish scales. Hind wing greyish-fuscous; cilia concolorous with a pale basal line; underside mottled with ochreous-white. Legs ochreous-white banded and suffused with greyish-fuscous.

Male genitalia.—See figure (Slide No. AB 21 September, 32).

Female genitalia.—Unknown.

Type.—U. S. N. M. No. 62745.

Type locality.—COSTA RICA: Tuis (5800 ft.).

Remarks.—Described from the ♂ type, 28.viii.08 (*Wm. Schaus*).

This specimen bears a label in Busck's handwriting, "(*Eulia*) *smaragditis* Meyr. Comp. w. *type*. AB June 1932". Superficially this specimen resembles *smaragditis*, but a comparison of the figures of the genitalia will serve to distinguish the two. Actually *subolivata* is much more closely related to *olivata*, but the transtilla of *subolivata* lacks the lateral processes found in *olivata*, the cornuti are much finer and the terminal portion of the gnathos is stouter.

Orthocomotis smaragditis (Meyrick) **comb. nov.**

(Pl. I, figs. 2–2*b*; Pl. V, fig. 6.)

Eulia smaragditis Meyrick, 1912, *Exotic Microlepidoptera* **1**: 11; *in* Wagner, 1912, *Lepidopterorum Catalogus*, Pt. 10: 38; *in* Wytsman, 1913, *Genera Insectorum*, fasc. 149: 38; 1926, *Exotic Microlepidoptera* **3** (8): 249.

Male genitalia.—See figures (Slide No. 6310).

Female genitalia.—As figured (Slide No. 10286).

Type.—In the British Museum (Natural History).

Type locality.—ARGENTINA: Parana.

Remarks.—Of this common species I have a series of 45 specimens (13 ♂, 32 ♀) from BRAZIL as follows: Nova Teutonia, ii–viii (*Fritz Plaumann*); New Bremen, ix. (*Fritz Hoffmann*); Rio Grande do Sul, Santa Cruz (no date or collector); Parana, no date (*F. Johnson*); Santa Catharina, 22.viii.35 (*Fritz Hoffmann*); São Paulo, Alta da Serra, x.23 (*Pohl*).

Orthocomotis aglaia sp. n.

(Pl. V, fig. 1.)

Alar expanse, 28 mm.

Labial palpus white; second segment overlaid with blackish-fuscous except apex and narrowly on the inner side; third segment with blackish-fuscous band around middle. Antenna fuscous except underside of scape which is white. Head blackish-fuscous; face, few scales at base of antenna and side, white. Thorax shining mouse grey; apex of tegula and posterior tuft fuscous, the latter with a few white scales mixed. Ground colour of forewing white, practically obscured by other markings; dark markings of forewing, except as noted below, deep mouse grey, these markings shining and with a violaceous hue, as follows: a broad band on dorsum from base to near middle; from basal fifth an outwardly curved fascia to fold and thence to near middle of cell; a fascia from middle of costa nearly to cell where it almost meets an inwardly oblique, elongate blotch from tornus; a preapical, costal spot confluent with an outwardly oblique bar from vein 7 to vein 2; all the dark markings and exposed areas of ground colour profusely marked by short black bars and spots; along fold, in areas between dark markings, at the end of cell and before termen much shining malachite green scaling; cilia white and fuscous mixed. Hind wing greyish-fuscous, except costal area; cilia concolorous with pale basal line; underside mottled with ochreous-white. Legs white to ochreous-white banded and suffused blackish-fuscous. Abdomen greyish-fuscous above, pale ochreous-white, irrorate with fuscous beneath.

Male genitalia.—Unknown.

Female genitalia.—As figured (Slide No. 10300).

Type.—U. S. N. M. No. 62742.

Type locality.—BRAZIL: Itatiaya, Est. do Rio (700 m.).

Remarks.—Described from the ♀ type, 12.x.1926 (*J. F. Zikan*, No. 156). Apparently nearest *leucothorax* and *smaragditis*, but distinguished from *leucothorax* by its dark thorax, from *smaragditis* by its dark coloured head and from both by the shining mouse-grey colouring of the fore wing. The female genitalia place *aglaia* nearest *smaragditis*.

Orthocomotis leucothorax sp. n.

(Pl. I, fig. 6.)

Alar expanse, 22 mm.

Labial palpus ochreous-white suffused with greyish-fuscous, except tips of second and third segments. Antenna, greyish-fuscous except the ochreous-white scape, the latter marked above with greyish-fuscous. Head buff, strongly infuscated above and with a greyish-fuscous frons; face ochreous-white. Thorax and ground colour of forewing ochreous-white; prothorax, base and apex of tegula and posterior tuft greyish-fuscous; base of tegula mixed with blackish-fuscous and yellowish-green scales; dark markings of fore wing greyish-fuscous as follows: a series of small spots on costa; from basal fifth of costa a fascia extends to fold thence outwardly to near middle of cell; a subquadrate blotch on middle of costa; from apical fifth of costa a broad blotch narrows and extends to vein 3 slightly before termen and one extension of it is confluent with tornal blotch near end of cell; a small spot in middle of dorsum; shining metallic malachite green scales overlay the basal costal half, centre and end of cell; yellowish-green scales scattered in tornal and preterminal areas; numerous blackish scales scattered over surface of wing; cilia pale yellowish mixed with greyish-fuscous. Hind wing greyish-fuscous, scales upturned giving a roughened appearance; cilia concolorous tipped with ochreous-white and with a pale basal line; underside mottled with ochreous-white. Legs ochreous-white banded and suffused with fuscous.

Male genitalia.—See figure (Slide No. 6299).

Female genitalia.—Unknown.

Type.—U.S. N. M. No. 62746.

Type locality.—BRAZIL: New Bremen.

Remarks.—Described from the ♂ type, 6.vi.36 (*Fritz Hoffmann*). Similar in habitus to *magicana* (Zeller), but easily distinguished from it by the dark coloured frons. The prolonged anellus of *leucothorax* and long, curved aedeagus further distinguish it from *magicana*.

Orthocomotis herbacea sp. n.

(Pl. III, figs. 6–6*a*.)

Alar expanse 23–24 mm.

Labial palpus ochreous-white; second segment suffused with greyish-fuscous outwardly; third segment with greyish-fuscous median annulus. Antenna greyish-fuscous, scape ochreous-white beneath. Head buff, slightly infuscated above; below antennae greyish-fuscous in centre, chocolate on each side; face ochreous white. Thorax cinnamon-buff, ochreous-white laterally; base of tegula fuscous overlaid with malachite green, apex fuscous; posterior tuft fuscous mixed with ochreous-white. Forewing ground colour ochreous-white; dark markings fuscous as follows: from basal fifth a broad oblique fascia to fold thence to centre of cell; a large oval spot on centre of costa; a large blotch from apical third of costa nearly to apex extending to vein 3; a spot on anal angle and a larger, oblique blotch before tornus beginning on vein 1b and extending past lower angle of cell; a narrow transverse bar at mid-termen; heavy green scaling on base of costa, along fold, between costal fascia and mid-costal spot, in tornus and beyond end of cell; around termen and tornus to middle of dorsum, greenish-yellow scales overlying chocolate spots; some chocolate scaling along veins. Hind wing greyish-fuscous, the scales upturned giving a roughened appearance; cilia concolorous with a light basal line; underside mottled with ochreous-white. Legs ochreous-white banded and suffused with greyish-fuscous; foretarsi and midtibia with chocolate spots.

Male genitalia.—See figures (Slide No. AB, Feb., 1920).
Female genitalia.—Unknown.

Type.—U. S. N. M. No. 62751.
Type locality.—Costa Rica: San Pedro de Montes de Oca.
Food plant.—Avocado.
Remarks.—Described from the ♂ type, 15.i.1933 (*C. H. Ballou*) and one ♂ paratype, Costa Rica: Mount Poas (*Wm. Schaus*). Paratype in the U.S. National Museum.

The type bears a handwritten label as follows: " Moth, reared on avocado, San Pedro de Montes de Oca, Costa Rica, Dec. 22, 1932. Pupated Jan. 1, 1933. Adult emerged Jan. 15, 1933. Charles H. Ballou ". This is the only species of the group for which there is any indication of the host plant.

There is a close resemblance between *herbacea* and *magicana*, but the roughened hind wing of the former immediately distinguishes it from the latter. The striking white midsection of the thorax, and the white markings of the fore wing of *magicana* further distinguish the two.

Orthocomotis magicana (Zeller) **comb. nov.**

(Pl. III, figs. 1–1*a*; Pl. VI, fig. 5.)

Penthina (*Sericoris*) *magicana* Zeller, 1866, *Stettin. ent. Ztg.* **27** : 150, pl. 1, fig. 9.
Eulia magicana (Zeller), Meyrick, 1926, *Exotic Microlepidoptera* **3** : 249.

Male genitalia.—See figures (Slide No. AB, 24.iv.26).
Female genitalia.—As figured (Slide No. AB, 24.iv.26).

Type.—In the British Museum (Natural History).
Type locality.—" Colombia."
Remarks.—Under this name I place eight specimens as follows: Colombia: ♀ (no date or exact locality given—from the Grace H. and John L. Sperry collection); Costa Rica: Juan Vinas, 3000 ft. 2 ♂, 28.viii.08; Mount Poas, 2 ♂, ♀; Cachi, 2 ♀. (All collected by *Wm. Schaus.*)

Orthocomotis twila sp. n.

(Pl. II, figs. 3–3*b* ; Pl. VI, fig. 1.)

Alar expanse, 20–23 mm.

Labial palpus ochreous-white ; second and third segments almost wholly suffused with greyish-fuscous. Antenna greyish-fuscous with chocolate scaling on base of shaft and on upper side of scape ; scape ochreous-white beneath. Head greyish-fuscous with ochreous-white scales mixed laterally ; area below antennae chocolate ; face ochreous-white. Thorax ochreous-white ; prothorax fuscous with chocolate and yellowish scales mixed ; base of tegula chocolate mixed with scattered green scales ; apex greyish-fuscous ; posterior tuft mixed light tawny and greyish-fuscous. Forewing ground colour ochreous-white ; costa narrowly yellowish with a series of dark spots ; dark markings of forewing fuscous, ill-defined, as follows : from basal fifth of costa a broad oblique fascia extends to centre of cell ; from middle of costa a moderately large blotch extends to cell ; a large tornal blotch extends to cell and base of vein 4 ; an outwardly oblique bar from vein 7, near cell, to vein 3 before termen ; a preapical, triangular spot ; from middle to end of cell a slender longitudinal white line ; in terminal area several, short, transverse white bars ; dark areas somewhat overlaid with chocolate and considerable green scaling along fold, and costa, in cell and at end of cell ; scattered dark spots throughout give the wing a mottled appearance and obscure the other usually well defined markings ; cilia yellowish, mixed with fuscous. Hind wing greyish-fuscous, except whitish costal area ; cilia mostly paler with a light basal line ; underside mottled with ochreous-white. Legs ochreous-white banded and suffused greyish-fuscous ; foretarsi with chocolate scaling. Abdomen light greyish-fuscous above, ochreous-white beneath spotted and suffused with fuscous in posterior half.

Male genitalia.—See figures (Slide No. 10431).

Female genitalia.—As figured (Slide No. 10434).

Type.—U. S. N. M. No. 62740.

Type locality.—BRAZIL : Nova Teutonia.

Remarks.—Described from the ♂ type, ii.1948 ; 10 ♂ and one ♀ paratypes as follows : BRAZIL : Nova Teutonia, 10 ♂, ♀, ii–vi.1948 (*Fritz Plaumann*) and viii.1936 (*H. S. Parish*). Paratypes in the U.S. National Museum, British Museum (Natural History) and the Naturhistorisches Museum, Vienna.

In male genitalia *twila* appears nearest to *melania*, but differs from it by the much coarser cornuti and broader transtilla. The female genitalia place it near *magicana*, from which *twila* differs by the narrower ostium and absence of any sclerotised areas in the bursa. The chief character which distinguishes *twila* is the lack of well defined markings, the whole fore wing having a mottled, nondescript appearance.

Orthocomotis ochrosaphes sp. n.

(Pl. II, figs. 2–2*a*.)

Alar expanse, 20 mm.

Labial palpus ochreous-white ; second segment suffused with greyish-fuscous except apex ; third segment with a median greyish-fuscous annulus. Antenna greyish-fuscous ; scape white beneath and with a chocolate spot above, near base. Head light tawny above, ochreous-white laterally, fuscous below antennae ; face ochreous-white. Thorax tawny mixed anteriorly with fuscous and throughout with scattered ochreous-white and fuscous scales. Forewing with dark markings fuscous or greyish, the fuscous markings as follows : an oblique fascia from basal fifth of costa to fold, thence outwardly curved to near the centre and upward to upper edge of cell where it almost meets a blotch on middle of costa ; a blotch on inner angle ; a small spot on tornus with a slender angulate line extending to end of cell at middle of wing ; a triangular mark from vein 3 to costa slightly before apex ; several small spots on dorsum ; before termen considerable white mixed with fuscous and yellowish-green scales ; at basal third of costa, above fold, and in centre of cell, white mixed with scattered fuscous and yellowish-green scales ; along fold four fuscous spots overlaid with shining green scales ; at base of costa, middle of cell and beyond end of cell similar green spots ; over surface of wing, particularly in outer half, clear, well defined ochreous-orange spots ; cilia greyish-fuscous mixed with ochreous-white. Hind wing, except costal area, greyish-fuscous ; cilia concolorous, paler apically and with a pale basal line ; underside mottled with ochreous-white. Legs ochreous-white (foreleg almost pure white) banded and suffused with fuscous. Abdomen light greyish-fuscous above, underside and posterior tuft buff, the former with two blackish-fuscous longitudinal lines and ochreous-orange scaling.

Male genitalia.—See figure (Slide No. 10443).

Female genitalia.—Unknown.

Type.—U. S. N. M. No. 62747.

Type locality.—BRAZIL : Santa Catharina.

Remarks.—Described from the ♂ type, 27.xii.35 (*Fritz Hoffmann*). This appears to be nearest *twila*, but is readily distinguished from it by the ochreous scaling of the fore wing.

Orthocomotis melania sp. n.

(Pl. II, figs. 5–5*a*.)

Alar expanse, 22 mm.

Labial palpus ochreous-white ; second segment suffused with light greyish-fuscous outwardly ; third segment similarly infuscated. Antenna greyish-fuscous with chocolate scaling on base of shaft above and on upper part of scape ; scape ochreous-white beneath. Head greyish-fuscous above with some buff scales mixed, fuscous below antennae ; face ochreous-white. Thorax light greyish-fuscous, whitish laterally ; prothorax and base of tegula mixed with chocolate, yellowish and green scales ; tegula beyond base whitish and apex greyish-fuscous. Ground colour of forewing ochreous-white ; costa narrowly yellowish ; dark markings fuscous as follows : a series of spots on costa and dorsum ; from basal fifth an oblique fascia to middle of cell ; from middle of costa an oblique fascia extends to vein 3 above tornus and is nearly confluent with a rectangular pretornal blotch ; from costa at apical third a broadening, oblique fascia extends almost to termen between veins 2 to 6 ; a preapical triangular spot ; a narrow area from base of wing along dorsum ; the dark areas are overlaid with chocolate and light paris green scales ; cilia ochreous-white mixed with greyish-fuscous. Hind wing greyish-fuscous, except white costal area, and scales upturned giving a roughened appearance ; cilia concolorous, tipped with ochreous-white and with a pale basal line ; *cubital pecten present* ; underside not mottled. Legs ochreous-white, banded and suffused with greyish-fuscous. Abdomen pale greyish-fuscous above, darker posteriorly, ochreous-white beneath ; on underside four blackish-fuscous median spots posteriorly.

Male genitalia.—See figures (Slide No. 10302).

Female genitalia.—Unknown.

Type.—U. S. N. M. No. 62750.

Type locality.—JAMAICA : St. Ann Parish (1750 ft.)

Remarks.—Described from the ♂ type, no date indicated (*Mr. and Mrs. E. L. Bell*).

This species is also remarkable for having a cubital pecten on the hind wing and in this respect is similar to *cristata*. It appears, however, that *melania* is actually more nearly related to *twila*, from which it differs by the rough scaling of the hind wing, the narrower transtilla and the extremely minute cornuti.

Orthocomotis muscosana (Zeller) **comb. nov.**

(Pl. IV, figs. 7–7*a*.)

Penthina (*Sericoris*) *muscosana* Zeller, 1866, *Stettin. ent. Ztg.* **27** : 148, pl. 1, fig. 8.
Eulia muscosana (Zeller) Meyrick, 1926, *Exotic Microlepidoptera* **3** : 249.

Male genitalia.—See figure (Slide No. 6298).

Type.—In the British Museum (Natural History).

Type locality.—" COLOMBIA."

Remarks.—I do not have a specimen of this species before me, but dissected the type and reproduce here a sketch of the harpe and aedeagus (by Bradley).

Orthocomotis boscantina (Dognin) **comb. nov.**

(Pl. III, figs. 5–5*a*.)

Tortrix boscantina Dognin, 1912, *Heterocères L'Amerique du Sud* **6** : 48.

Male genitalia.—See figure. (Slide No. AB, 22 March, 1926.)
Female genitalia.—Unknown.

Type.—In the U.S. National Museum.

Type locality.—COLOMBIA : San Antonio, Cali.

Remarks.—On the type label, written by Dognin, the trivial name is spelled " *boscantica* " as is the name on a label, attached to the pin, written by Durrant.

As far as I know this species is represented only by the type and is distinguished from other species of the genus by the preponderance of white scaling and the group of ochreous-orange scales beyond the cell of the forewing.

Orthocomotis argodonta sp. n.

(Pl. IV, fig. 6.)

Alar expanse, 30 mm.

Labial palpus white ; second segment overlaid blackish-fuscous outwardly, except apex ; third segment blackish-fuscous except base. Antenna fuscous, except scape, which is blackish-fuscous above, white beneath. Head black with few white scales mixed ; face white. Thorax and ground colour of forewing white ; prothorax, posterior tuft, base and apex of tegula blackish-fuscous ; posterior tuft with a few white scales ; dark markings blackish-fuscous and mostly confluent, almost obliterating the white ground colour ; four large, and several small, spots on costa white ; dorsum white, three tooth-like projections extending into the blackish-fuscous central part of wing ; on middle of dorsum a moderate-sized spot ; sparse emerald green scaling on dark portions of wing ; cilia white, obscured along termen by blackish-fuscous. Hind wing light greyish-fuscous, darker apically ; costal area whitish ; underside mottled ; cilia greyish-fuscous with pale basal line and some scattered pale scales. Legs ochreous-white suffused and spotted with greyish-fuscous. Abdomen mixed greyish-fuscous and white above, ochreous-white beneath.

Male genitalia.—Unknown.

Female genitalia.—As figured (Slide No. 10299).

Type.—U. S. N. M. No. 62741.

Type locality.—Brazil : Santa Catharina.

Remarks.—Known only from the type, no date (*F. Johnson*). A striking species with no apparent closely associated species in the genus. The colouring and widely separated ovipositor lobes immediately set it apart from all the others.

Orthocomotis citroleuca (Meyrick) **comb. nov.**

Cnephasia citroleuca Meyrick, 1912, *Trans. ent. Soc. Lond.* **1911** : 683.

Type.—In the British Museum (Natural History).

Type locality.—Colombia : San Antonio, 5800 ft.

Remarks.—The abdomen of the type is missing, but the species undoubtedly belongs in this group. The species is known only from the type.

Orthocomotis cristata sp. n.

(Pl. III, fig. 7.)

Alar-expanse, 22 mm.

Labial palpus ochreous-white ; second segment suffused with light fuscous outwardly. Antenna greyish-fuscous ; scape dark vinaceous-brown above, ochreous-white beneath. Head ochreous-white infuscated above and dark vinaceous-brown below antennae. Thorax and ground colour of forewing ochreous-white ; prothorax and base of tegula fuscous mixed with yellowish and greenish scales, remainder suffused with greyish-fuscous ; dark markings of forewing fuscous, somewhat suffused with reddish, as follows : along costa six or seven spots extending to cell and outwardly limited by vein 10 ; from basal fifth of costa an irregular, curved fascia to lower edge of cell then outwardly curved to centre ; a large, longitudinal oval blotch from end of cell to termen ; a spot from base of wing to basal fourth of dorsum ; a blotch extending from tornus to cell ; some light infuscation in central half of wing ; from base, along fold to middle, an elongate vinaceous-brown bar ; all dark areas more or less clothed with scattered yellowish-green scales ; cilia ochreous-white mixed with greyish-fuscous. Hind wing fuscous ; cilia greyish-fuscous with pale basal line ; *cubital pecten present ;* underside not mottled. Legs ochreous-white banded and suffused with greyish-fuscous.

Male genitalia.—See figure (Slide No. CH, 0–3).

Female genitalia.—Unknown.

Type.—U. S. N. M. No. 62744.

Type locality.—Costa Rica : Cachi.

Remarks.—Described from the ♂ type, no date (*Wm. Schaus*). Distinguished from all other species of the genus, except *melania*, by, and remarkable for, the presence of the cubital pecten.

Orthocomotis smaragdophaea (Meyrick) **comb. nov.**

(Pl. I, figs. 4–4*a* ; Pl. V, fig. 2.)

Eulia smaragdophaea Meyrick, 1932, *Exotic Microlepidoptera* 4 (9) : 258.

Male genitalia.—See figures (Slide No. 10294).

Female genitalia.—As figured (Slide No. 10295).

Type.—In the Naturhistorisches Museum, Vienna.

Type locality.—BRAZIL : "Jaragua and New Bremen."

Remarks.—Meyrick placed this species near *muscosana* but, as a comparison of the genitalia clearly shows, they are not closely related.

Under this name I place the following specimens from BRAZIL : Nova Teutonia, 3 ♂, 5 ♀, May to August dates (*Fritz Plaumann* ; *H. S. Parish*) ; Santa Catharina, 2 ♀ (*Fritz Hoffmann*) ; Itatiaya, Est. do Rio, 700 m., ♂, 9.xi.1931 (*J. F. Zikan*).

Orthocomotis scardiana (Dognin) **comb. nov.**

(Pl. II, figs. 6–6*a*.)

Orthotaenia (?) *scardiana* Dognin, 1905, *Ann. Soc. ent. Belg.* **49** : 86.
Eulia scardiana (Dognin), Meyrick, 1912, *in* Wagner, *Lepidopterorum Catalogus*, Part 10 : 38 ; 1913, *in* Wytsman, *Genera Insectorum*, fasc. **149** : 38.

Male genitalia.—See figures (Slide No. AB, 20 Mar., 1926).

Female genitalia.—Unknown.

Type.—In the U.S. National Museum.

Type locality.—ECUADOR : El Monje près Loja.

Remarks.—Doubtfully placed here and probably requiring a new genus.

PLATE I.

FIGS. 1, 1*a*.—*Orthocomotis melanochlora* (Meyrick). (1) Ventral view of male genitalia with left harpe and aedeagus removed. (1*a*) Lateral aspect of aedeagus.

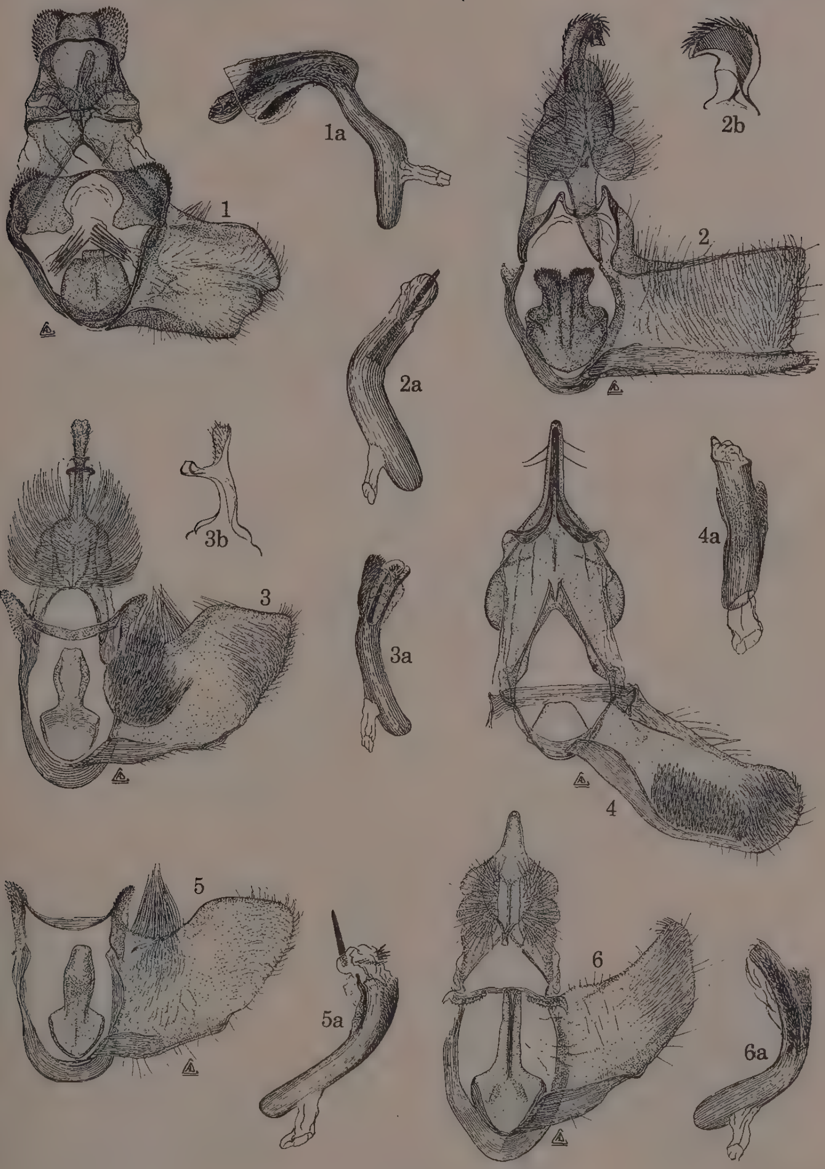
FIGS. 2, 2*b*.—*O. smaragditis* (Meyrick). (2) Ventral view of male genitalia with left harpe and aedeagus removed. (2*a*) Lateral aspect of aedeagus (there are two long cornuti, one superimposed over the other). (2*b*) Detail of uncus.

FIGS. 3–3*b*.—*O. mareda* sp. n. (3) Ventral view of male genitalia with aedeagus and left harpe removed. (3*a*) Lateral aspect of aedeagus. (3*b*) Detail of uncus.

FIGS. 4, 4*a*.—*O. smaragdophaea* (Meyrick). (4) Ventral view of male genitalia with left harpe and aedeagus removed. (4*a*) Lateral aspect of aedeagus.

FIGS. 5, 5*a*.—*O. jordani* sp. n. (5) Ventral view of male genitalia showing right harpe, transtilla, anellus and vinculum. (5*a*) Lateral aspect of aedeagus.

FIGS. 6, 6*a*.—*O. leucothorax* sp. n. (6) Ventral view of male genitalia with left harpe removed. (6*a*) Lateral aspect of aedeagus.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The genus *Orthocomotis* Dognin.

PLATE II.

Figs. 1, 1*b*.—*Orthocomotis chaldera* (Druce). (1) Ventral view of male genitalia with left harpe and aedeagus removed. (1*a*) Lateral aspect of aedeagus. (1*b*) Lateral outline of uncus and gnathos.

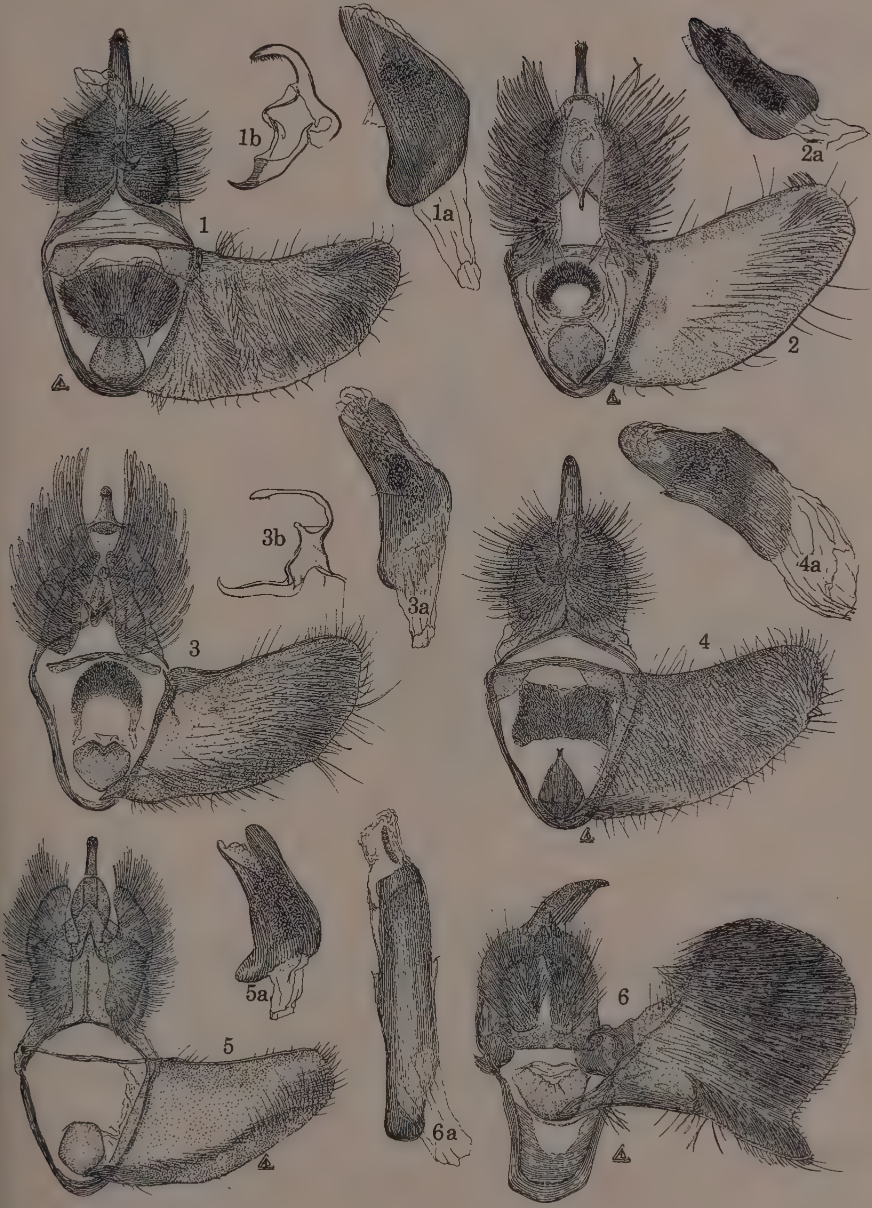
Figs. 2, 2*a*.—*O. ochrosaphes* sp. n. (2) Ventral view of male genitalia, with left harpe and aedeagus removed. (2*a*) Lateral aspect of aedeagus.

Figs. 3, 3*b*.—*O. twila* sp. n. (3) Ventral view of male genitalia with left harpe and aedeagus removed. (3*a*) Lateral view of aedeagus. (3*b*) Lateral outline of uncus and gnathos.

Figs. 4, 4*a*.—*O. ochracea* sp. n. (4) Ventral view of male genitalia with left harpe and aedeagus removed. (4*a*) Lateral aspect of aedeagus.

Figs. 5, 5*a*.—*O. melania* sp. n. (5) Ventral view of male genitalia with left harpe and aedeagus removed. (5*a*) Lateral aspect of aedeagus.

Figs. 6, 6*a*.—*O. scardiana* (Dognin). (6) Ventral view of male genitalia with left harpe and aedeagus removed. (6*a*) Lateral aspect of aedeagus.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The genus *Orthocomotis* Dognin.

PLATE III.

Figs. 1, 1*a*.—*Orthocomotis magicana* (Zeller). (1) Ventral view of male genitalia with left harpe and aedeagus removed. (1*a*) Lateral aspect of aedeagus.

Fig. 2.—*O. subolivata* sp. n. Right harpe.

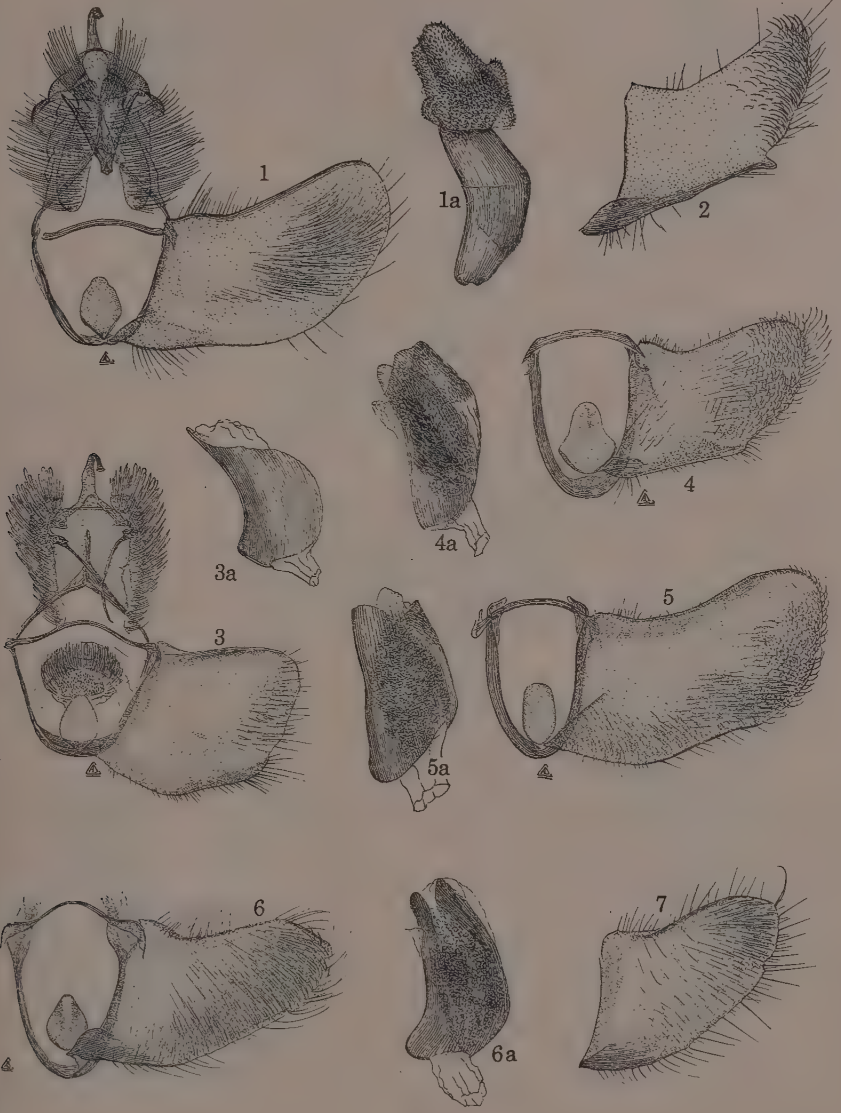
Figs. 3, 3*a*.—*O. pseudolivata* sp. n. (3) Ventral view of male genitalia with left harpe and aedeagus removed. (3*a*) Lateral aspect of aedeagus.

Figs. 4, 4*a*.—*O. herbaria* (Busck). (4) Ventral view of right harpe, transtilla, anellus and vinculum. (4*a*) Lateral aspect of aedeagus.

Figs. 5, 5*a*.—*O. boscantina* (Dognin). (5) Ventral view of right harpe, transtilla, anellus and vinculum. (5*a*) Lateral aspect of aedeagus.

Figs. 6, 6*a*.—*O. herbacea* sp. n. (6) Ventral view of right harpe, transtilla, anellus and vinculum. (6*a*) Lateral aspect of aedeagus.

Fig. 7.—*O. cristata* sp. n. Right harpe.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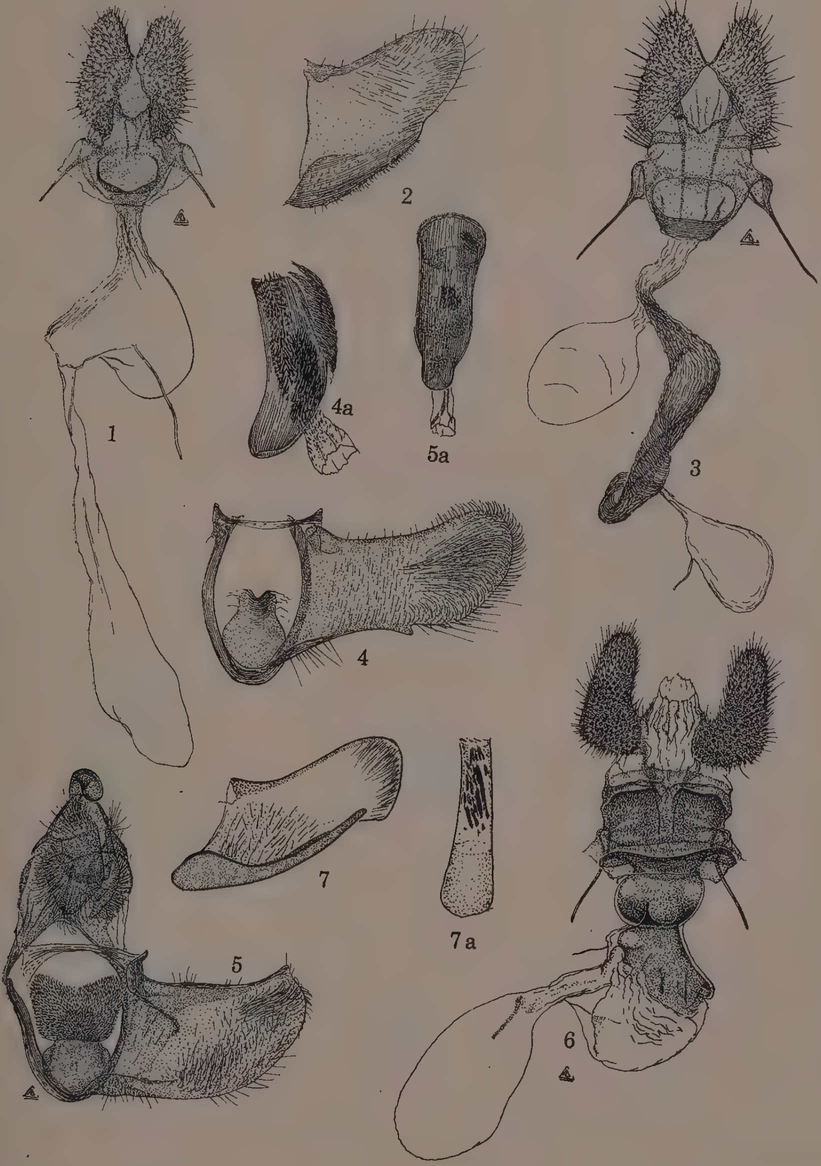
The genus *Orthocomotis* Dognin.

PLATE IV.

Fig. 1.—*Orthocomotis herbaria* (Busck). Ventral view of female genitalia.
Fig. 2.—*O. nitida* sp. n. Right harpe.
Fig. 3.—*O. prochaldera* sp. n. Ventral view of female genitalia.
Figs. 4, 4*a*.—*O. olivata* Dognin. (4) Ventral view of right harpe, transtilla, anellus and vinculum. (4*a*) Lateral aspect of aedeagus.
Figs. 5, 5*a*.—*O. euchaldera* sp. n. (5) Ventral view of male genitalia with left harpe and aedeagus removed. (5*a*) Ventral view of aedeagus.
Fig. 6.—*O. argodonta* sp. n. Ventral view of female genitalia.
Figs. 7, 7*a*.—*O. muscosana* (Zeller). Right harpe. (7*a*) Aedeagus.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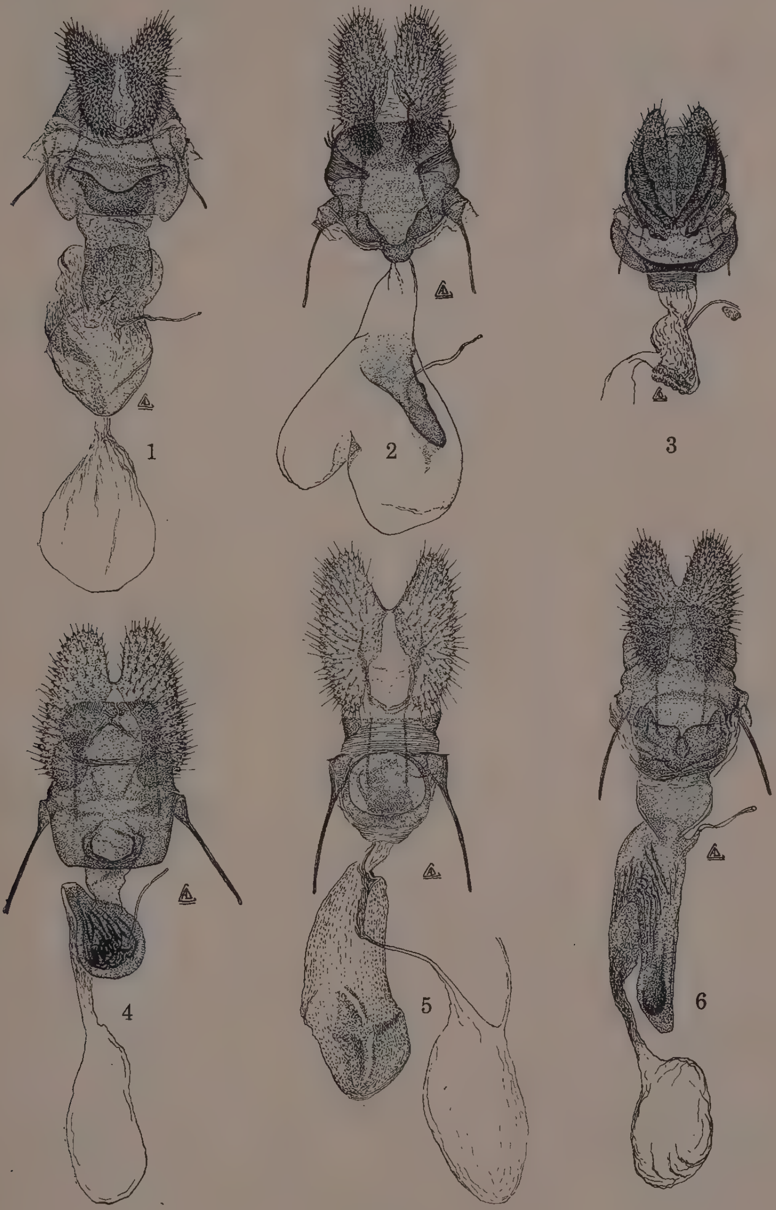
The genus *Orthocomotis* Dognin.

PLATE V.

Ventral views of female genitalia.

FIG. 1.—*Orthocomotis aglaia* sp. n.
FIG. 2.—*O. smaragdophaea* (Meyrick).
FIG. 3.—*O. melanochlora* (Meyrick) (bursa copulatrix removed).
FIG. 4.—*O. mareda* sp. n.
FIG. 5.—*O. olivata* Dognin.
FIG. 6.—*O. smaragditis* (Meyrick).



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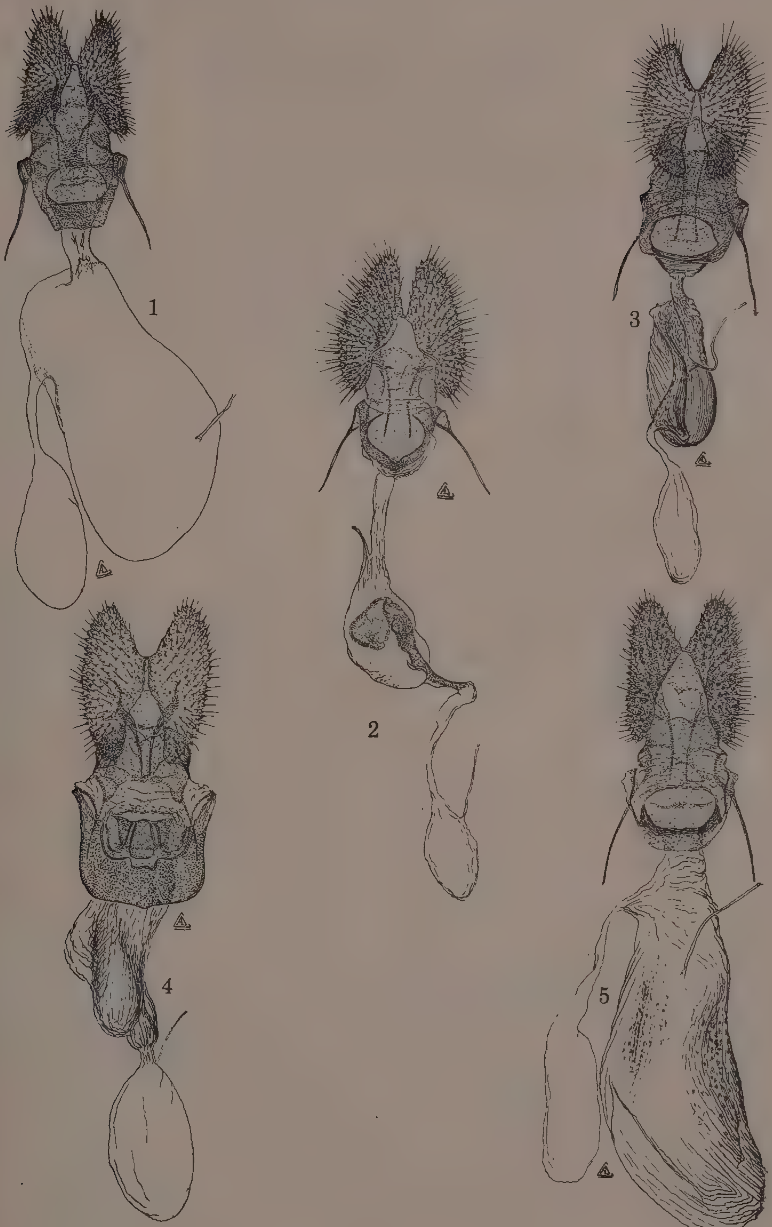
The genus *Orthocomotis* Dognin.

PLATE VI.

Ventral views of female genitalia.

Fig. 1.—*Orthocomotis twila* sp. n.
Fig. 2.—*O. pseudolivata* sp. n.
Fig. 3.—*O. chaldera* (Druce).
Fig. 4.—*O. exolivata* sp. n.
Fig. 5.—*O. magicana* (Zeller).



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The genus *Orthocomotis* Dognin.

Referring to the poor state of our knowledge of the morphology of Lepidoptera :

" North American entomologists, the fortunate—from an entomological point of view—possessors of crop-destroying insects, have done a great deal in this branch of our science."

(Jordan, K., 1898, *Novit. zool.* **5** : 374.)

" What special sensation these palpal and caputal organs [the chaetosema and other organs in Lepidoptera] are adapted to perform, we do not know. Insects possibly have less sense than the higher mammals, but probably more senses."

(Jordan, K., 1923, *Novit zool.* **30** : 158.)

" There is no line to draw between good and bad definitions, sufficient and insufficient descriptions ; and every description is incomplete."

(Jordan, K., 1903, *Novit. zool.* **9** (suppl. : xi.))

REVISIONS OF THE GENERA OF MALLOPHAGA. *COLILIPEURUS* BEDFORD AND A NEW GENUS.

By Theresa Clay.
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With 1 Plate and 51 Text Figures.

Introduction.

The genus *Colilipeurus* was erected by Bedford (1930 : 167) for the distinctive Ischnoceran species found on the bird order Coliiformes. These species are characterised by the form of the head and of the tergal plates of the abdomen, the presence of a vulval fringe, the distinctively-shaped alveoli of the lateral setae of the female genital region, the form of the male terminal abdominal segments and genitalia. Setae with rather similar elongated alveoli are found on the female genital region of some species of *Pectinopygus* (e.g. *P. bassani*), and *Vernoniella* has a vulval fringe, but there is no other described group of species which in any way resembles *Colilipeurus*. However, three new species parasitising the genus *Microhierax* of the order Falconiformes are found to have the characters listed above which distinguish *Colilipeurus* from other known genera. In the male sex the two groups further resemble one another in the form of the antenna and in the general form of the genitalia, especially in the paramere which has a partly free sclerite articulating with the basal plate and which allows the considerable backward movement of the paramere for the copulatory position. In the female both groups have a similar arrangement of the lateral genital setae, no sclerotised calyx in the spermatheca and individuals with and without central tergal sclerotisation (see below). In fact, the only significant differences are the shape of the coni of the nymphs, and in the adults the abdominal chaetotaxy, the form of the abdominal sclerites and differences in the sclerotisation of the whole exoskeleton, the species from *Microhierax* being more heavily sclerotised. It is the resulting colour pattern which makes the two groups of species so distinct at a casual glance (Plate I). Colour pattern, however, is an unsatisfactory character for generic separation, as shown by such genera as *Quadraceps* and *Philopterus*, where it seems to be dependent on the colour of the plumage of the hosts. The similarity in basic characters of the two groups is the more remarkable in that they are characters which are not of a generalized kind found in other genera of the Mallophaga, but are extremely distinctive and never or rarely found elsewhere in the suborder. These facts suggest that the two groups are related and that the similarity cannot be explained by any form of convergence or parallel evolution. It is possible that the two groups should not be separated generically, but on taking into account their distribution, their superficial distinctive appearance, the difference in the abdominal sclerites and chaetotaxy, and in the nymphs, together with the fact that there is no overlap of these characters between the species of the two groups, suggests that it would be more satisfactory to place the species from *Microhierax* in a different genus. It is, however, not unlikely that the taxon may later be considered to be no more than a subgenus, if this category (which indicates difference without hiding relationships) should prove a useful one in Mallophaga.

Host Distribution.

The host distribution of these two groups is difficult to explain: *Colilipeurus* is found only on the Coliiformes, a small order geographically restricted, occurring only in the Ethiopian Region, and of doubtful affinities; *Microhierax*, a genus comprising five species found from the W. Himalayas to S.E. Asia, is included in a subfamily of the Falconiformes, the Polihieracinae which contains five genera found in S. America, Africa and Asia. Mallophaga have been seen from hosts belonging to four of these genera as follows: *Degeeriella sens. str.* from *Gampsonyx* (Argentina) and *Neohierax* (Burma), *Neopsittaconirmus* from *Polihierax* (Somaliland) and the new genus described below from *Microhierax* (Burma, Thailand and the Philippines). The specimens of *Neopsittaconirmus*, a distinctive genus hitherto found only on parrots, were taken from *Polihierax semitorquatus* under conditions which precluded any contamination during collecting. Eleven specimens of *Polihierax* were examined: no Mallophaga were taken from six of these, but 56 specimens were taken from the remaining five birds from three localities in British Somaliland; in no instance was a parrot collected on the same day. Mr. John G. Williams of the Coryndon Museum, Nairobi, says (*in litt.*) that in British Somaliland the parrot, *Poicephalus rufiventris*, roosts in nests of the buffalo weaver and that *Polihierax semitorquatus* takes over the old nests of this weaver for nesting purposes. Thus, the occurrence of *Neopsittaconirmus* might be a case of natural straggling on an exceptionally large scale, or the parrot parasites may have become established on the hawk.

Since there is no evidence of relationship between the Coliiformes and *Microhierax* and if the affinities of *Colilipeurus* and the new genus have been correctly evaluated, then a possible explanation of the distribution of these two genera would be that a parasite of an ancestral Coliiformes became established on a forerunner of *Microhierax* at a time when, it must be assumed the ranges of these birds overlapped. This establishment may have been assisted by the absence or rarity of a resident louse population on the small falcon, a factor which may also help to explain the occurrence at the present time of a parrot parasite on *Polihierax*. As both groups of Mallophaga now comprise a number of species it must be presumed that the interspecific transfer took place at a fairly remote date, the parasite species becoming differentiated on the different species of *Microhierax* as these became separated. The main differences between the two parasite groups are shown in the sclerotisation, probably an adaptation to the different plumage structure of the two host groups.

Microhierax is also parasitised by a species belonging to the Amblycera which does not belong to any of the genera typical of the Falconiformes, nor is it related to the characteristic *Colimenopon*, the only other genus found on *Colius*. No specimens of genera belonging to the Mallophagan fauna characteristic of the Falconiformes have been taken from *Microhierax*.

Abdominal Differences in the Females.

A casual glance at populations of species of both these genera suggests that among the fully hardened females there are two forms: one (group A) in which the divided tergal plates of some segments are joined by a central area of sclerotisation (figs. 22 and 41) and the other (group B) in which this central sclerotised area is absent (figs. 23 and 42). The question is whether this is dimorphism, an extra nymphal stage or an extended duration of the teneral condition. Females of a similar type are found in *Pectinopygus* and *Falcolipeurus*.

In the few species of Mallophaga of which adults have been reared under artificial conditions three nymphal instars were found, each instar increasing in size and in the complexity of the chaetotaxy. Wilson (1939 : 319) has drawn attention to the importance in *Lipeurus* of the postero-dorsal setae of the pterothorax for recognising the various instars. Metrical and morphological examinations of nymphs of a number of Ischnoceran genera confirm the presence of three nymphal instars and the importance of the pterothoracic setae : all first stage nymphs examined have on each side one elongated posterodorsal pterothoracic seta and a small, often spine-like, more lateral seta ; the second instar has more pterothoracic setae and the third has more and/or stouter setae, the numbers and position depending on the adult chaetotaxy. In those species in which the adult head is highly modified the first instar may have the marginal carina complete and unmodified or already somewhat resembling the adult head, but the fully modified head does not appear until after the last moult ; the ventral carina is usually in its adult form at least by the second stage. Abdominal sclerites are not apparent in the first instar, but the second and third instars frequently resemble each other and differ from the adult in having the tergal plates separated from the pleural plates, while in some genera (e.g. *Fulicoffula*) the tergites of IX and X appear as separate plates, not fused together as in the adult. Thus, even apart from the unsclerotised condition of most of the exoskeleton, there is no difficulty about distinguishing last stage nymphs from adults. A fairly detailed study has been made of nymphs and females of *Pectinopygus gyricornis* (Denny). The three usual nymphal stages are present. Amongst those specimens with the adult type of abdomen and head are the obviously teneral forms, over-lapping in abdomen length with the largest of the third instar nymphs, but distinct in the breadth of the temples ; lighter in general colour than the adults, with no sclerotised area between the tergites and with the abdominal segments compressed in an antero-posterior direction. The mean of the breadth of the head of group A and group B, including obvious tenerals, is the same. Excluding obvious tenerals and considering only adults which are similar in the dark colour of the sclerites, there is a range from those in which the irregular sclerotised areas completely fill the space between the tergites through those with smaller areas and those with very faint sclerotised areas, to those in which the cuticle between the tergal plates shows no sign of sclerotisation. Out of 51 females of *P. gyricornis* examined 28 had some sign of sclerotisation (group A) and 23 (including obvious tenerals) had no sign of sclerotisation (group B). None of group A had an abdomen less than 1.48 mm. long (maximum 1.69, coefficient of variation 3.4) and less than 0.70 mm. (maximum 0.85) wide. All these specimens had well developed ova in the abdomen. Group B had lower minimum measurements for the length and breadth of the abdomen : 1.20 mm. (maximum 1.55 mm., coefficient of variation 6.8) in length and 0.58 mm. (maximum 0.74 mm.[1]) in breadth.

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[1] Two specimens appeared to be larger than this, but had already been treated with KOH and mounted in canada balsam so that the measurements may not be comparable with those taken from specimens mounted in a saturated solution of phenol in 70 per cent. alcohol and warmed slightly to clear ; this method seems to cause little distortion and enables the ova to be measured within the abdomen. Space is not available to give the full measurements taken, but the results are based on length and breadth of head and abdomen.

The mean of both abdominal length and breadth was greater in group A. The majority of group B had no developed ova, and only one specimen (but the ova of two of the largest could not be measured) had ova of comparable size to those normal in group A.

In *Colilipeurus* and *Falcolius* gen. n., of which smaller series were available, there appears to be a comparable situation. In *Colilipeurus* the first instar has the typical pterothoracic setae, entire marginal carina and no apparent abdominal sclerites. The second instar has a small central hyaline margin; five pterothoracic setae each side, of which one is minute, one fine and long, one stout and long and two fine; there are more abdominal setae, and only the pleural plates are sclerotised. In the third instar the head is similar; the dorsal pterothoracic setae are still five in number but differ in position and size, and the elongated lateral pterothoracic seta with sunken alveolus is now present; the abdominal setae are more numerous and both tergal and pleural plates are sclerotised. Specimens which are adult in the form of the head, abdomen and chaetotaxy range from obviously teneral specimens without the central sclerotised strip, apparently normal adults without the strip (fig. 23), intermediates in which some of the tergal plates are joined and some only by faint sclerotised strips, to those with a fully sclerotised strip joining the two plates (fig. 22). A range of measurements similar in type to those for the *Pectinopygus* species was found: no difference in head breadth between group A and B, an overlap in length and breadth of abdomen, but with higher means for group A, all those in group A showing well developed ova and only a small number of group B with ova of a comparable size to those of A. Two pairs, the females each of group B, were found *in copula* and the majority of this group, with the exception of the obviously teneral specimens, had fairly well developed ova, a higher proportion than was the case of group B in the *Pectinopygus* species. In *Falcolius* only second and third instars of *F. jordani* and only third instars of *F. elbeli* are available; in the former species the second and third instars resemble one another and differ markedly from the adult and from the nymphs of *Colilipeurus* (fig. 20) in having sclerotised recurved and pointed coni (fig. 21) which resemble those of the adults of some species of *Paragoniocotes*. In the second instar there is a small hyaline margin; the lateral pterothoracic seta is present and there are four dorsal setae each side, of which one is minute, two fine and long, and one stout and long; pleural and tergal plates are present. The third instar has the head similar to that of the second instar, the pterothoracic setae in the adult number and positions but less stout, and the abdomen (except for the larger size and the greater number of setae) is similar to that of the second instar; the smallest specimen of this instar measured was longer than the largest of the second by 0·18 mm. There are also a number of pharate adults[2] which in the male have the genitalia apparently complete but unsclerotised, and in the female the elongated lateral setae of segments IX–X present, but unsclerotised. Amongst 27 females of *F. jordani* 15 belong to group A (fig. 41) and 12 to group B (fig. 42); there are no intermediates. The range and means of the measurements are comparable with those of *Pectinopygus* and *Colilipeurus*; little evidence is available about the size of the ova, but at least one female of group B had ova of comparable size to one of group A.

These results suggest that the cause of the apparent dimorphism of the females is the same in the three genera examined and that the central sclerotised area of the abdomen is formed during the hardening and stretching of the teneral abdomen; that in some cases this process is either not fully completed (e.g. mature females of *Pectinopygus gyricornis* with small and faint areas) or there is no sclerotisation of this area (e.g. full-sized females with fully-developed ova and without sclerotisation) or the sclerotisation of this area may be a long process which continues after the adult is mature and begins to lay eggs. A decision on these alternatives must wait for the examination of further material, especially of *Colilipeurus* and *Falcolius* and the following of the stages in artificially maintained populations.

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[2] Pharate adult is a third stage nymph immediately before its moult which shows the adult still enclosed within the skin of the 3rd instar (see Hinton, 1946 : 552).

COLILIPEURUS Bedford.

Colilipeurus radiatus (Neumann), 1912. (Plate I, figs. 1–2; text-figs. 1–4, 6–7, 10, 12, 14, 16–17, 22–26.)

Lipeurus radiatus Neumann, 1912, *Arch. Parasit.* **15**: 378, figs. 23–26. Host: Undetermined birds nos. 30 and 32 collected in Harar, Abyssinia.
Lipeurus radiatus nun Neumann, 1912, *Arch. Parasit.* **15**: 380. Host: *Ploceus abyssinicus*.

The specimens on which Neumann based his descriptions of *Lipeurus radiatus* and *L. nun* were taken from three birds collected on the same day by M. de Rothschild at Harar. The two undetermined birds must have been either *Colius striatus hilgerti* Zedlitz or *C. m. macrourus* (Linn.) and the single female taken from *Ploceus abyssinicus* on the same day must have been a straggler from a *Colius*. Dr. J. Dorst of the Muséum National d'Histoire Naturelle in Paris has most kindly searched for the two undetermined birds numbered 30 and 32, but has been unable to find them and believes them to have been destroyed. It has not been possible, either, to trace the type material of Neumann's forms and it is therefore necessary to try to identify them from his original descriptions. The species from *Colius striatus* and *C. macrourus* differ in the shape of the head, the parameres of the male and the sclerites of the female genital region. Although Neumann's figure of a whole female *radiatus* appears to resemble, in the shape of the head, the female of the species found on *macrourus*, there is no doubt that the figure of the male genitalia represents those of the species from *C. striatus*. It can, therefore, be presumed with reasonable certainty that the male of *radiatus* at least is the species normally found on *Colius striatus* and redescribed below. If the type material should be found, it is presumably a specimen of this sex which will be designated as lectotype. The figure of the female, which may represent a teneral specimen of either the species found on *C. striatus* or *C. macrourus* is of the type with the unjoined tergal plates (see above), while the single specimen from which *radiatus nun* was described was a female with the joined tergal plates and can be assumed to be the same as *radiatus*.

Male (Plate I, fig. 1 and text-figs. 1–4, 6–7, 10, 12, 16): The dorsal surface of the head has many minute setae not present in the female. Dorsal prothoracic pigmented patch (fig. 12) usually present. Post-spiracular setae are present on segments III–VIII[3] with contiguous sensilli (Clay, 1954: 716) on III–V; tergocentral setae stout and pointed, both

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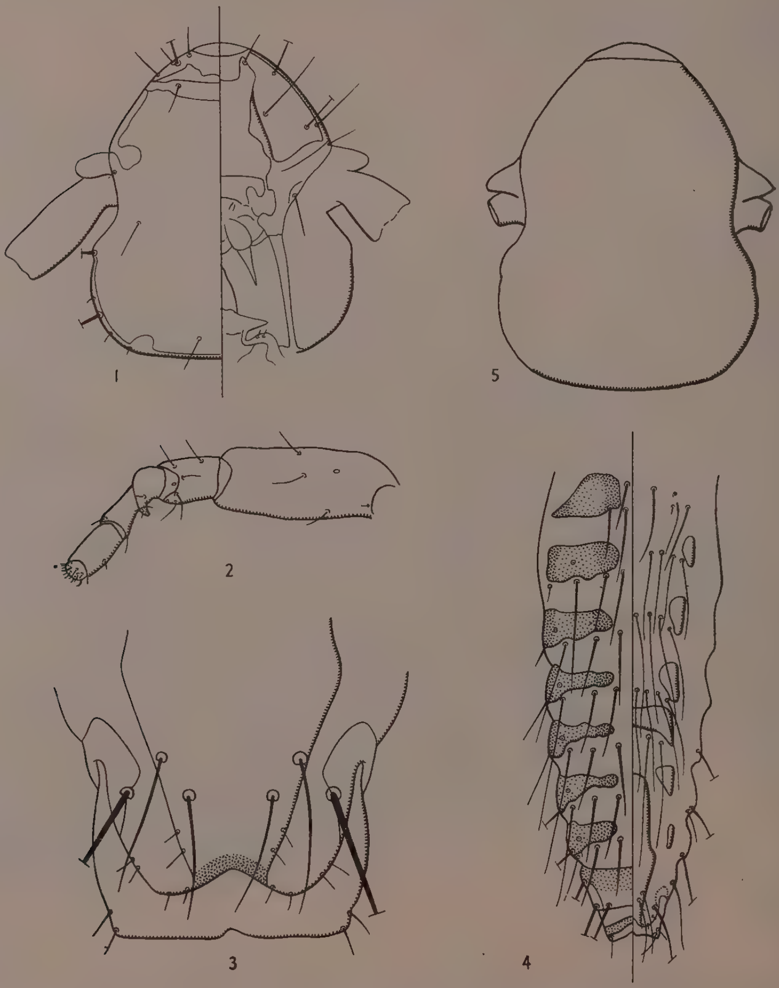
[3] First apparent abdominal segment is segment II.

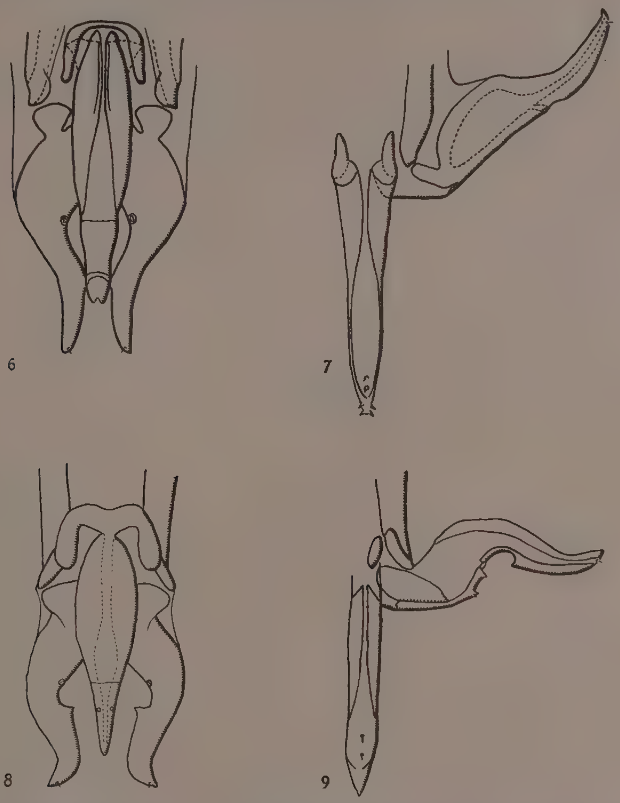
these and the sternal setae may vary in number by one to three a segment. The male genitalia are complicated in structure and two views of these are shown (figs. 6–7) as the sclerites appear very different in the resting and copulatory positions. Measurements of both sexes shown in Tables I–II.

Female (Plate I, fig. 2 and text-figs. 14, 17, 22–26): Tergocentral setae stout and pointed as in the male; post-spiracular setae and sensilli as in the male. The variation in the form of the tergites has been discussed above. Variation of tergocentral setae as follows: II, 6 or 7; III–V, 8 or 9 (rarely 6 or 7): VI–VII, 6 or 7.



Figs. 1–5.—(1–4) *Colilipeurus r. radiatus*, ♂. (1) Head. (2) Antenna. (3) Terminal segments of abdomen, ventral. (4) Abdomen, dorsal and ventral. (5) *C. c. colius*, outline of head, scale as in 1.

Specimens examined: 43 males and 55 females from *Colius striatus* subspp. from Kenya, Uganda, N. Rhodesia and Cape Colony.



Figs. 6–9.—Male genitalia. (6) *C. r. radiatus*, resting position, dorsal. (7) As 6, extruded, ventral. (8) *C. c. colius*, resting position, dorsal. (9) As 8, extruded, ventral.

Colilipeurus radiatus **obscurior** subsp. n. (Text-figs. 13, 15, 18–19, 27.)

Type host: *Colius colius* (Linn.).

Only one male of this form is available, the genitalia of which appear to be the same as those of the nominate form. The subspecies differs in both sexes in the form of the gular plate (figs. 18–19), which varies in outline but in general is smaller and narrower, and in having the pigmented areas of the thorax larger (figs. 13, 15). The postero-ventral margin of the abdomen of the single male is more deeply and narrowly indented and the sclerites of the female genital region differ in shape (fig. 27). For measurements see Table I–II.

Described from 1 ♂, 6 ♀ from *Colius colius* Potchefstroom, W. Transvaal, 4.iv.1953.

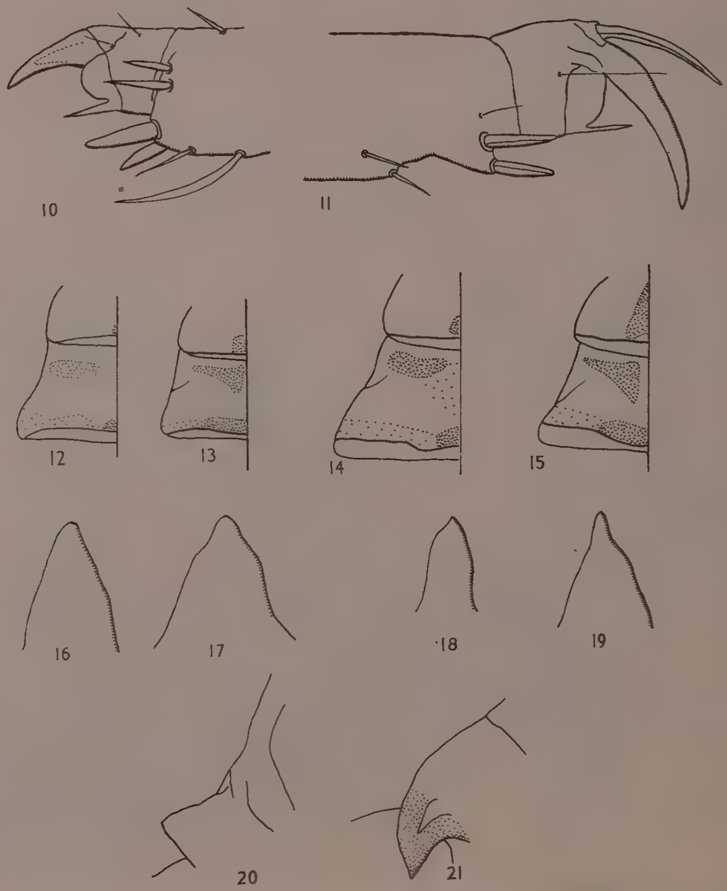
Holotype male in the South African Institute for Medical Research, Johannesburg. *Paratypes*: 6 ♀. All type material with the above data.

Colilipeurus colius (Bedford), 1920. (Text-figs. 5, 8–9, 11, 20, 28, 29.)

Type host: *Colius indicus transvaalensis* Roberts.

Esthiopterum colius Bedford, 1920, *Rep. vet. Res. S. Afr.* 7–8 : 731, pl. 7, figs. 1, 2. Host: *Colius indicus.*

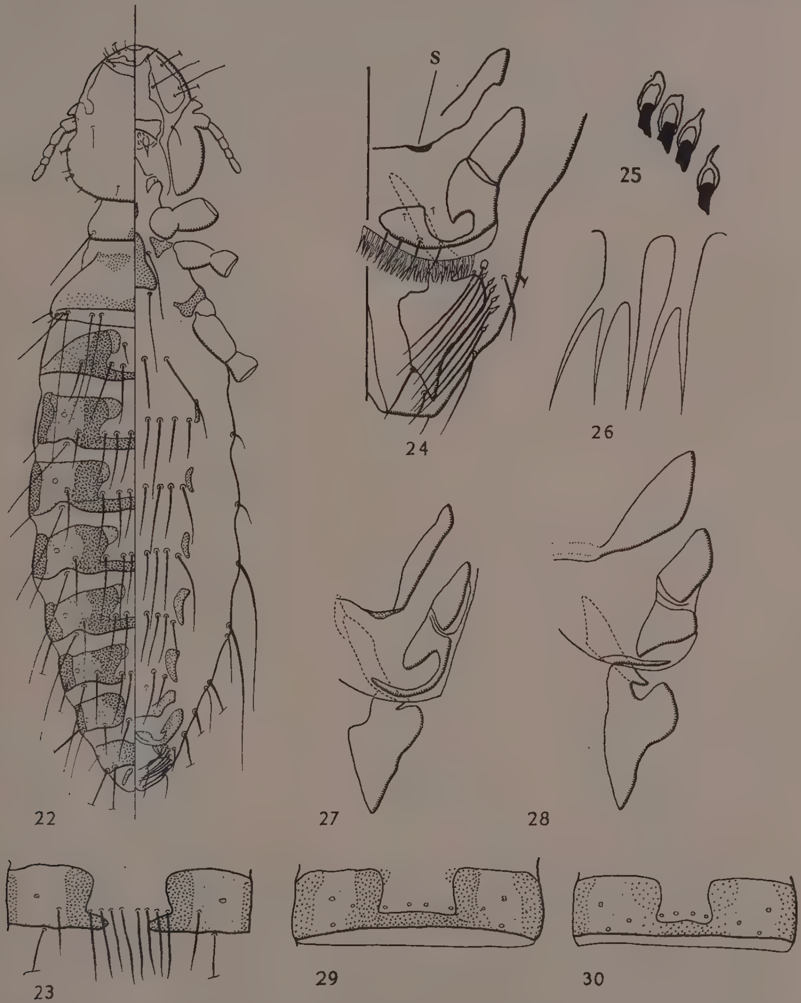
Male: Distinguished from *radiatus* by the proportions of the head (fig. 5) and by the male genitalia, especially in the shape of the paramere and the presence of two to three small thorn-like hyaline protuberances on its inner margin (figs. 8–9). Prothorax usually without dorsal posterior pigmented area. Sternite VI is interrupted medianly. Measurements shown in Table I.



Figs. 10–21.—(10–11) Terminal part of legs. (10) *Colilipeurus r. radiatus*, first leg. (11) *C. c. colius*, third leg. (12–15) Dorsal view of thorax. (12) *C. r. radiatus*, ♂. (13) *C. r. obscurior*, ♂, (14) *C. r. radiatus*, ♀. (15) *C. r. obscurior*, ♀. (16–19) Gular plates. (16) *C. r. radiatus*, ♂. (17) As 16, ♀. (18) *C. r. obscurior*, ♂. (19) As 18, ♀. (20–21) Conus of nymph. (20) *C. c. colius*. (21) *Falcolius jordani*, pharate ♀.

Female : Distinguished from *radiatus* by having the prothoracic pigmented patch greatly reduced or absent, in the details of the sclerites of the female genital region (fig. 28) and in the absence of a crescent-shaped thickening each side of the posterior margin of the genital plate (fig. 24, s). Measurements shown in Table II. Abdomen usually with 2–3 fewer tergocentral setae on each of segments III–V than in *radiatus*.

Specimens examined : 27 ♂, 30 ♀ from *Colius indicus* subspp. from King William's Town, Cape Colony, Transvaal and S.W. Africa.

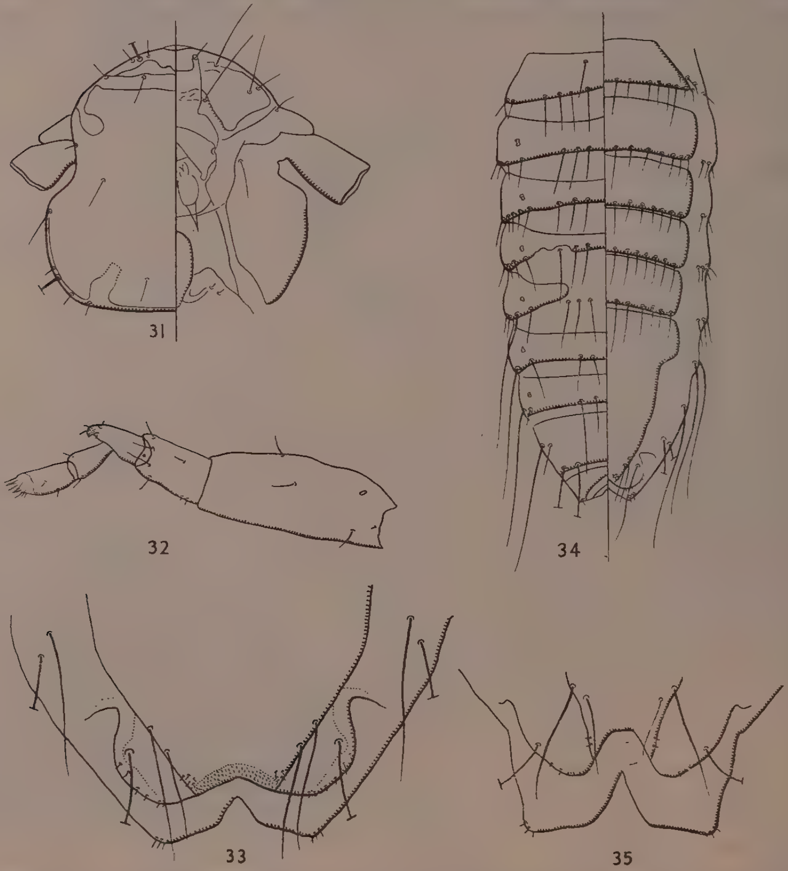


Figs. 22–30.—(22–26) *Colilipeurus r. radiatus*, ♀. (22) Dorsal and ventral views. (23) Tergum of abdominal segment III, teneral specimen. (24) Genital region. (25) Alveoli of lateral setae of segments IX–X. (26) Elements of vulval fringe. (27–28) Sclerites of ♀ genital region. (27) *C. r. obscurior*. (28) *C. c. colius*. (29–30) Tergum of abdominal segment IV, ♀. (29) *C. c. colius*. (30) *C. c. pallidior*.

Colilipeurus colius **pallidior** subsp. n. (Text-fig. 30.)

Type host: *Colius macrourus macrourus* (Linn.).

The populations from *Colius macrourus* are separable from *Colilipeurus colius* by the smaller and lighter sclerotised areas and in the means of the measurements. In the male there is no sclerotised patch on the pterothorax, the genital plate is not easily seen except in heavily stained specimens and the whole of the sclerotised areas are lighter in colour. In the female the pterothoracic patch is smaller, as is also the inner vertical sclerotised area of the tergites (fig. 30); as in the male all the sclerotised areas are lighter in colour. The measurements tend to be smaller, but there is a certain amount of overlap (Tables I–II). Populations differing only in the mean of the measurements should not, in the opinion of the present writer (Clay, 1955 : 5),[4] be separated subspecifically, but in this



Figs. 31–35.—(31–34) *Falcolius jordani*, ♂. (31) Head. (32) Antenna. (33) Terminal segments of abdomen, ventral. (34) Abdomen, dorsal and ventral views. (35) *F. samarensis*, terminal segments of ♂ abdomen, ventral.

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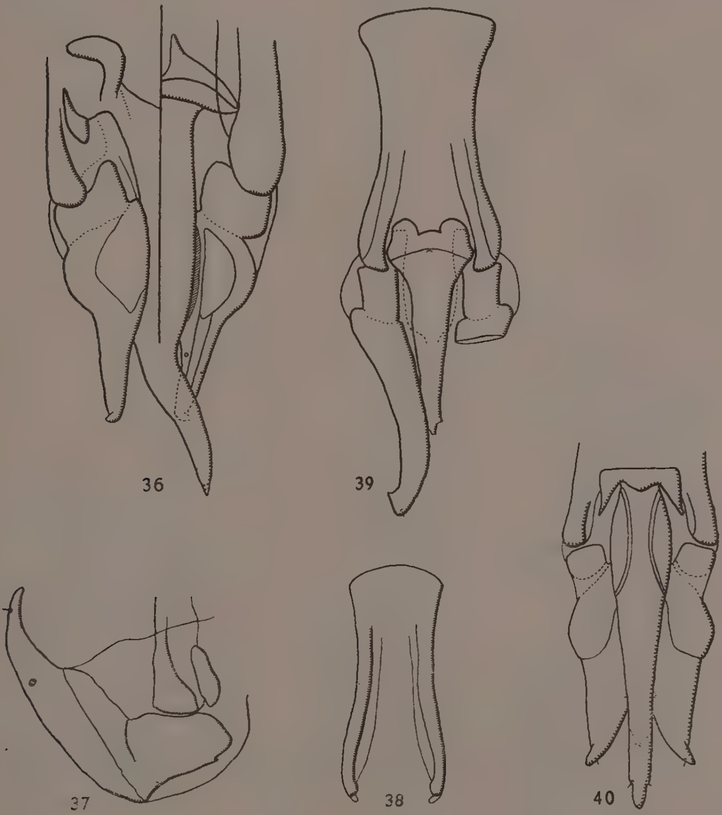
[4] On page five of this paper somehow between manuscript and final printing the word "not" has managed to insinuate itself into line twenty-six, which should, of course, read "which on the different hosts differ only in size in proportion to".

case the smaller size is accompanied by differences in sclerotisation and a subspecies has therefore been erected for the *macrourus* population.

Holotype male and *allotype* female : slide no. 17071a in the Meinertzhagen Collection in the British Museum (Natural History) from *Colius m. macrourus* from Port Sudan. *Paratypes* : 37 males and 28 females with the same data.

Colilipeurus as now known comprises four taxa which show a range of sclerotisation from the most heavily sclerotised form, *C. r. obscurior* through *C. r. radiatus* and *C. c. colius* to the most lightly sclerotised *C. c. pallidior*. The differences are slight and are found chiefly in the extent of the thoracic dorsal sclerotised areas. The relationships between the taxa of *Colilipeurus* reflect those usually accepted for their hosts, that is *Colius striatus* and *C. colius* being included in one species group (or the genus or subgenus *Colius*) and *C. indicus* and *macrourus* in another species group (or the genus or subgenus *Urocolius*). Each species group is parasitised by a species of *Colilipeurus* with a subspecies



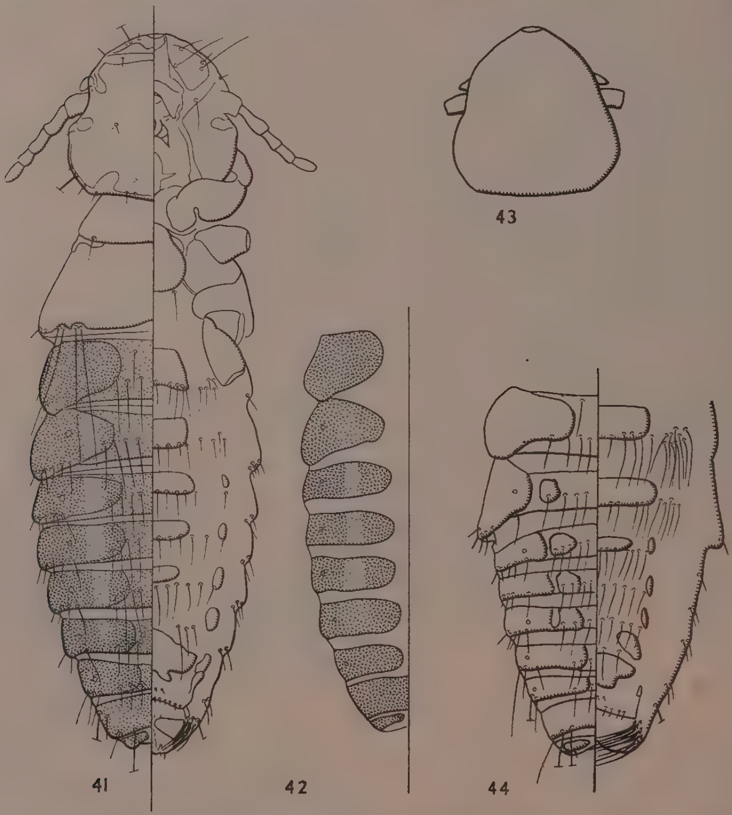
Figs. 36–40.—♂ genitalia of *Falcolius* species. (36) *F. jordani*. (37) *F. jordani*, paramere in extruded position. (38) *F. jordani*, basal plate. (39) *F. samarensis*. (40) *F. elbeli*.

on each of the included host species ; no Mallophaga have been seen from two of the species of the *striatus* group.

FALCOLIUS gen. n.

Elongated Ischnocera. Marginal carina depressed centrally with small hyaline margin, central part enlarged dorsally and ventrally, dorsal enlargement with indented posterior margin ; ventral carina interrupted medianly and prolonged towards anterior margin each side ; transverse dorsal preantennal suture. Temple with only one elongated seta. Abdominal segments II–IV, at least, with central sternal plates ; male with tergal plates II–V continuous across segment ; female tergites without inner vertical sclerotised area (contrast figs. 22 and 41). Male with ventral genital opening of characteristic form (fig. 33). Female with vulval fringe and with ventral group of long stout setae with irregular, elongated alveoli, each side of segments IX–X (figs. 47–49).

Type species : *Falcolius jordani* sp. n.
Distribution : The genus *Microhierax* of the order Falconiformes.
The gender of the genus is masculine.



Figs. 41–44.—(41–42) *Falcolius jordani*. (41) ♀, dorsal and ventral views. (42) Tergum of abdomen of teneral ♀. (43) *F. elbeli*, ♀ head, scale as in **41**. (44) *F. elbeli*, ♀ abdomen.

Affinities: Apparently closely allied to *Colilipeurus*, from which it can be separated by the presence of central sternal plates on abdominal segments II–IV, the abdominal chaetotaxy, the form of the tergites, and in the nymphs by the coni. *Colilipeurus* itself has no obvious affinities to any other known genus and reflects the isolated position of its host order, the Coliiformes.

Falcolius jordani sp. n. (Pl. I, figs. 3 and 4; text-figs. 21, 31–34, 36–38, 41–42, 47–49.)

Type host: *Microhierax caerulescens burmanicus* Swann.

This species is distinguished from the other two known species of the genus in the male by the genitalia and in the female from *elbeli* by the form of the abdomen and from *samarensis* by the shape of the head and details of the chaetotaxy.

Male (Plate I, fig. 3, and text-figs. 31–34, 36–38): The dorsal surface of the head has minute setae as in *C. radiatus*. Fine post-spiracular setae on segments III–VIII with contiguous sensilli on segments III–V. The margin of the genital opening has fine serrations. The male genitalia, as in the species from *Colius*, are complicated and the apparent shape of the sclerites varies according to the position on the slide and whether the parameres are in the turned-back position (fig. 37). In fig. 36 the penis is shown fully extended, in many specimens it appears shorter, due to being bent back on itself. Variation of chaetotaxy shown in Table V and measurements in Table III.

Female (Plate I, fig. 4 and text-figs. 41–42, 47–49): There is some individual variation in the shape of the subvulval sclerite (fig. 48). This species differs from *elbeli* in having the cuticle surrounding the opening of the spermathecal tube sclerotised. Variation of chaetotaxy shown in Table VI, and measurements in Table IV.

Holotype male and *allotype* female slide no. 628 in the British Museum (Natural History) from *Microhierax caerulescens burmanicus* from Myitkyina, Burma, 16.iii.1945. *Paratypes*: 28 males and 22 females from the same host form from Burma and Thailand.

This species is named in honour of Dr. Karl Jordan, F.R.S., as a small tribute to a great entomologist and in particular to his unique contributions to the study of ectoparasites.

Falcolius samarensis sp. n. (Text-figs. 35, 39, 45, 51.)

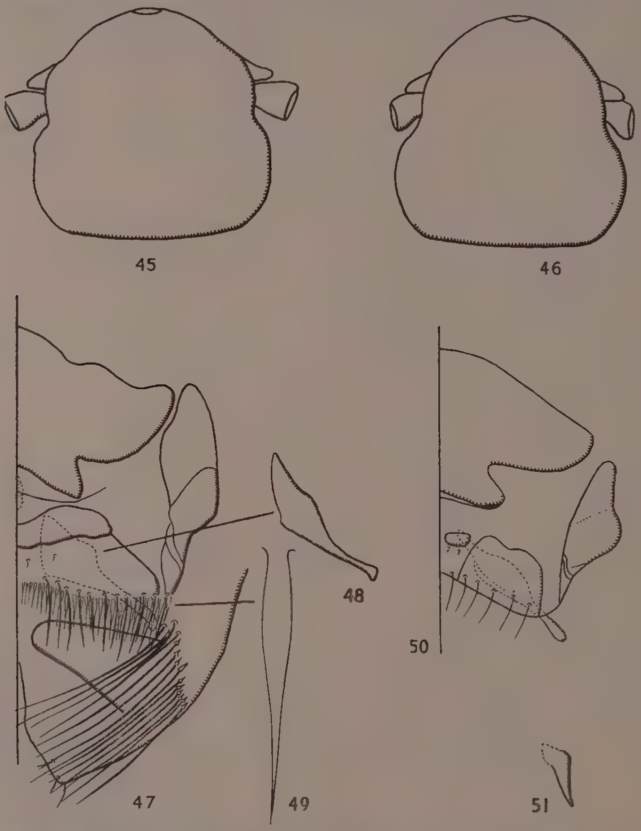
Type host: *Microhierax erythrogonys meridionalis* Ogilvie-Grant.

This species is distinguished from *jordani* in the male by the genitalia and in the female by the shape of the head, the apparent absence of the genital plate, form of the vulval fringe and by the details of the abdominal chaetotaxy; it differs from *elbeli* in the male by the genitalia and in the female by the form of the abdomen.

Male: Resembles that of *jordani* except in size (Table III), the form of the last segment (fig. 35) and the genitalia (fig. 39). The single male is not in sufficiently good condition to compare the form of the tergal plates with those of *jordani*. The abdominal chaetotaxy of the single male is shown in Table V and measurements in Table III.

Female: Similar to that of *jordani*, but the head is proportionally narrower across the preantennal region and resembles that of *elbeli* (fig. 43). The tergal plates are less heavily sclerotised, there is no apparent genital plate nor any other sclerite associated with the genital region except for the subvulval sclerite of which only the distal part can be clearly distinguished (fig. 51). The parts of the vulval fringe are bifid or trifid as in *Colilipeurus*, there are fewer of the elongated lateral genital setae (9 + 9) and there is a small amount of sclerotisation round the spermathecal opening. The abdominal chaetotaxy of the single female is shown in Table VI; this differs from that of *jordani* in the fact that the central sternal setae of segment III are all minute, the pleural setae fewer in number and the seta immediately lateral to the post-spiracular seta on each side of segment VI long and stout. Chaetotaxy as shown in Table VI and measurements in Table IV.

Holotype male and *allotype* female slide no. 629 in the British Museum (Natural History) from *Microhierax erythrogonys meridionalis* from Samar Island, Philippines 21.vi.1948 presented by Mr. G. H. E. Hopkins.



Figs. 45–51.—(45–46) Outline of ♂ head, scale as in fig. 31. (45) *Falcolius samarensis.* (46) *F. elbeli.* (47–49) *F. jordani,* ♀. (47) Genital region. (48) Subvulval sclerite from another specimen. (49) Element of vulval fringe. (50) *F. elbeli,* ♀ genital region. (51) *F. samarensis,* subvulval sclerite.

Falcolius elbeli sp. n. (Text-figs. 40, 43–44, 46, 50.)

Type host: *Microhierax fringillarius* (Drapiez).

This species is distinguished from the two preceding ones in the male by the genitalia and in the female by the form of abdominal segments II and III.

Male : Similar to that of *jordani* but differs in the shape of the head (fig. 46), size (Table III) and in the characters of the male genitalia (fig. 40). Segment VI may have an irregular-shaped sclerotised area between the two tergal plates. The abdominal chaetotaxy is shown in Table V.

Female : Head similar to that of *jordani* but differs in shape (fig. 43). The abdomen (fig. 44) differs markedly from that of the two preceding species in the enlargement of segments II and III and from *jordani* in the division of the tergal plates of III and IV into two sclerites each side, such a division being only indicated in the latter species. Ventrally segments II–III have central sclerites, IV (and in one specimen, V) a central and two lateral sclerites and V or VI–VII lateral sclerites only. The genital region is similar to that of *jordani*, but the shapes of the sclerites are different (fig. 50) and there is no sclerotisation round the spermathecal opening. Variation of the chaetotaxy shown in Table VI and measurements in Table IV.

Holotype male and *allotype* female in the British Museum (Natural History) from *Microhierax fringillarius* from Prachuap Khiri Khan, Thailand, 24.xii. 1952. *Paratypes* : three males and six females from the same host species from Borneo, Malaya and Thailand.

This species is named after Mr. Robert E. Elbel in grateful thanks for the loan of specimens of this species and of a large series of *jordani* which made a full study of the new genus *Falcolius* possible.

Key to **Colilipeurus** and **Falcolius**.

1		Abdominal segments II–IV without central sternal plates ; ♂ with tergites II–IV interrupted medianly ; ♀ with less than 10 setae on 2nd sternum	(**Colilipeurus**) 2
–		Abdominal segments II–IV, at least, with central sternal plates; ♂ with tergites II–IV not interrupted medianly ; ♀ with more than 10 setae on 2nd sternum	(**Falcolius**) 9
2	(1)	Males	3
–		Females	6
3	(2)	Inner edge of paramere with pointed projection	4
–		Inner edge of paramere without pointed projection	5
4	(3)	Pterothorax without central postero-dorsal pigmented area	**c. pallidior**
–		Pterothorax with small postero-dorsal pigmented area . . .	**c. colius**
5	(3)	Prothoracic and pterothoracic central pigmented areas large (fig. 13)	**r. obscurior**
–		Prothoracic (if present) and pterothoracic areas half the size (fig. 12)	**r. radiatus**
6	(2)	Crescent-shaped thickenings on posterior margin of genital plate absent	7
–		The above character present	8
7	(6)	Inner vertical sclerotised area of tergites reduced . .	**c. pallidior**
–		Inner vertical sclerotised area of tergites not reduced . . .	**c. colius**
8	(6)	Prothoracic dorsal pigmented area reaching to anterior margin of prothorax	**r. obscurior**
–		Prothoracic pigmented area not reaching above middle of prothorax	**r. radiatus**
9	(1)	Males	10
–		Females	12
10	(9)	Penis in resting position not reaching beyond parameres .	**samarensis**
–		Penis in resting position reaching beyond parameres	11

11 (10) Total length under 1·60 mm.; total length of genitalia under 0·40 mm.; genitalia as in fig. 40 . . . . **elbeli**

– Total length over 1·80 mm.; total length of genitalia over 0·50 mm.; genitalia as in fig. 36 . . . . **jordani**

12 (9) Length of lateral sclerotised margin of abdominal segment III more than 2½ times that of IV; no central sternal plate on segment VI **elbeli**

– Length of margin of segment III less than twice that of IV; central sternal plate on segment VI 13

13 (12) Seta immediately lateral to post-spiracular seta on VI long and stout; elements of vulval fringe bifid or trifid. . . . **samarensis**

– Above seta short; elements of vulval fringe simple . . **jordani**

SUMMARY

The genus *Colilipeurus* and its affinities with a group of three new species from the avian genus *Microhierax* together with the problems of the host distribution are discussed. Some remarks on the sclerotisation of teneral specimens are included. The two known species of *Colilipeurus* are redescribed, and two new subspecies of this genus and a new genus with three new species are described.

ACKNOWLEDGMENTS.

I am indebted for the presentation and loan of material to Mr. Robert E. Elbel, North Eastern Thailand Malaria Control Adviser for the United States Operational Mission to Thailand; Dr. Henry S. Fuller, formerly of the U.S.A. Typhus Commission, Burma; Major E. L. Haydock of Luanshya, N. Rhodesia; Mr. G. H. E. Hopkins, Tring and Mr. H. E. Paterson of the South African Institute for Medical Research, Johannesburg. I also express my grateful thanks to Mr. G. H. E. Hopkins for helpful criticisms and suggestions.

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TABLE I.—*Measurements (mm.) of male* Colilipeurus *species in Canada Balsam.*

	r. radiatus.			*r. obscurior.*		*c. colius.*			*c. pallidior.*		
	Range.	Mean.		Range.		Range.	Mean.		Range.	Mean.	
Length :											
Head . .	0·36–0·40	0·38	(15)	0·37	(1)	0·37–0·40	0·375	(21)	0·33–0·37	0·35	(25)
Abdomen .	0·78–0·90	0·84	(9)	0·78	(1)	0·73–0·82	0·785	(20)	0·73–0·78	0·76	(21)
Total .	1·46–1·68	1·52	(9)	1·40	(1)	1·33–1·49	1·440	(20)	1·36–1·48	1·40	(20)
Genitalia .	0·31–0·32		(3)	.	.	0·28		(2)	0·26–0·29	0·27	(8)
Breadth :											
Head . .	0·31–0·34	0·32	(15)	0·28	(1)	0·27–0·30	0·29	(21)	0·25–0·28	0·27	(25)
Prothorax .	0·22–0·27	0·24	(9)	0·22	(1)	0·18–0·23	0·21	(20)	0·18–0·21	0·19	(22)
Pterothorax .	0·32–0·37	0·35	(8)	0·32	(1)	0·30–0·37	0·33	(20)	0·27–0·31	0·29	(19)
Abdomen .	0·30–0·38	0·33	(9)	0 28	(1)	0·28–0·35	0·31	(20)	0·23–0·29	0·27	(20)
Head Index .	0·80–0·87	0·84	(15)	0·76	(1)	0·73–0·79	0·76	(20)	0·74–0·83	0·77	(23)

Numbers in brackets denote numbers of specimens measured.

TABLE II.—*Measurements (mm.) of female** Colilipeurus *species.*

	r. radiatus.			*r. obscurior.*			*c. colius.*			*c. pallidior.*		
	Range.	Mean.		Range.	Mean.		Range.	Mean.		Range.	Mean.	
Length :												
Head .	0·45–0·48	0·47	(16)	0·42–0·45	0·44	(5)	0·45–0·52	0·48	(21)	0·43–0·46	0·44	(13)
Abdomen .	1·20–1·38	1·30	(15)	1·15–1·25	1·20	(4)	1·08–1·35	1·25	(20)	1·11–1·28	1·17	(12)
Total .	2·00–2·26	2·14	(14)	1·90–2·04	1·96	(4)	1·34–2·20	2·05	(20)	1·92–2·10	1·96	(12)
Breadth :												
Head .	0·37–0·42	0·40	(16)	0·35–0·37	0·36	(5)	0·33–0·40	0·38	(21)	0·34–0·38	0·36	(12)
Prothorax .	0·27–0·30	0·29	(14)	0·25–0·28	0·27	(5)	0·25–0·32	0·28	(20)	0·25–0·30	0·26	(12)
Pterothorax	0·47–0·52	0·50	(13)	0·42–0·45	0·43	(4)	0·42–0·53	0·49	(20)	0·38–0·48	0·43	(9)
Abdomen .	0·55–0·68	0·62	(15)	0·45–0·57	0·54	(5)	0·52–0·65	0·59	(19)	0·48–0·55	0·51	(12)
Head Index	0·79–0·91	0·84	(16)	0·80–0·86	0·83	(5)	0·73–0·81	0·78	(20)	0·78–0·84	0·81	(12)

* Females with central tergal sclerites. Numbers in brackets denote numbers of specimens measured.

TABLE III.—*Measurements (mm.) of male* Falcolius *species in Canada balsam.*

	jordani.			*elbeli.*			*samarensis.*
	Range.	Mean.		Range.	Mean.		Range.
Length :							
Head . .	0·44–0·47	0·46	(16)	0·40–0·43	0·420	(4)	0·41
Abdomen .	1·06–1·16	1·11	(7)	0·79	.	(2)	0·78
Total . .	1·87–2·01	1·95	(7)	1·51–1·52	1·515	(2)	1·52
Genitalia .	0·55–0·60*	0·58	(7)	0·32		(1)	0·36
Breadth :							
Head . .	0·45–0·47	0.460	(16)	0·38–0·42	0·405	(4)	0·42
Prothorax .	0·35–0·37	0·360	(10)	0·30–0·33	0·315	(2)	0·33
Pterothorax .	0·53–0·57	0·550	(7)	0·43–0·45	0·440	(2)	0·43
Abdomen .	0·52–0·53	0·525	(8)	0·38–0·40	0·390	(2)	0·42
Head Index .	0·96–1·05	1·01	(16)	0·90–1·00	0.970	(4)	1·02

* Variation depends partly on position of penis

TABLE IV.—*Measurements (mm.) of female* Falcolius *species in Canada Balsam.*

	jordani.				*elbeli.*		*samarensis.*
	Range.*	Mean.*	Range.†	Mean.†	Range	Mean.	Range.
Length:							
Head . .	0·50–0·53	0·52 (13)	0·47–0·52	0·50 (12)	0·48–0·50	0·50 (6)	0·50
Abdomen .	1·20–1·37	1·33 (9)	1·12–1·30	1·20 (9)	1·14–1·32	1·23 (4)	?‡
Total .	2·14–2·40	2·29 (9)	2·04–2·26	2·15 (11)	2·13–2·22	2·17 (4)	?
Breadth:							
Head . .	0·52–0·55	0·54 (13)	0·48–0·54	0·53 (12)	0·50–0·52	0·510 (6)	0·52
Prothorax .	0·43–0·48	0·45 (10)	0·42–0·45	0·44 (10)	0·43–0·45	0·440 (4)	0·45
Pterothorax .	0·68–0·75	0·71 (10)	0·63–0·70	0·67 (9)	0·67–0·68	0·675 (4)	0·72
Abdomen .	0·66–0·80	0·76 (10)	0·57–0·77	0·65 (10)	0·77–0·78	0·775 (2)	?
Head Index .	1·00–1·06	1·03 (13)	1·02–1·08	1·04 (12)	0·98–1·04	1·010 (6)	1·04

* With central tergal sclerite.
† Without central tergal sclerite.
‡ The single female was dissected before measurement.

TABLE V.—*Abdominal chaetotaxy of male* Falcolius.

	jordani.			*elbeli.*			*samarensis.*		
	Pl.	Tg.	St.	Pl.	Tg.	St.	Pl.	Tg.	St.
II . . .	0–4	7–8	17–22	0	6–7	15–18	0–1	4	16
III . . .	4–7	8–9	15–19	4–6	6–7	13–14	3	6	11
IV . . .	4–8	6–7	13–16	4	5–6	12	2–3	5	12
V . . .	4–7	5–8	12–15	4–5	4	11	2	4	9
VI . . .	4–6	6–7	11–14	4–5	4	10–12	3	4	10
VII . . .	3	5–6	0	2–3	4	0	3	4	0
VIII . .	2	4–5	0	2	4	0	2	4	0

Pl. = pleural. Those setae lateral to the post-spiracular setae (which are omitted from table) and given for one side only.

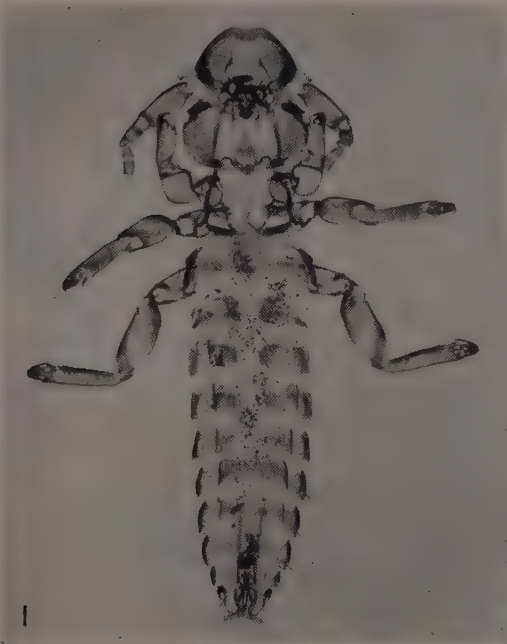
Tg. = tergal setae. The two anterior setae on segment II are omitted for all species.

St. = sternal setae.

TABLE VI.—*Abdominal chaetotaxy of female* Falcolius.

	jordani.			*elbeli.*			*samarensis.*		
	Pl.	Tg.	St.	Pl.	Tg.	St.	Pl.	Tg.	St.
II . .	0–3	7–9	18–24	0	8–10	30–33	?2	9	?19
III . .	6–10	7–12	15–19	6–8	8–11	17–22	5	10	?16
IV . .	7–10	8–12	13–17	5–6	9–12	12–19	3	9	12
V . .	4–9	7–9	11–16	5–4	8–9	12–15	3	9	10
VI . .	4–8	7–8	11–15	5–6	7–8	10–15	4	9	11
VII . .	2–3	4–6	6–7	3	7–8	5–6	3	7	10
VIII . .	2	4	*	2	4	*	2	4	*

See notes under Table V; sternal setae on segment VII include two minute setae.
* Sternal setae of VIII–XI as in figures or descriptions.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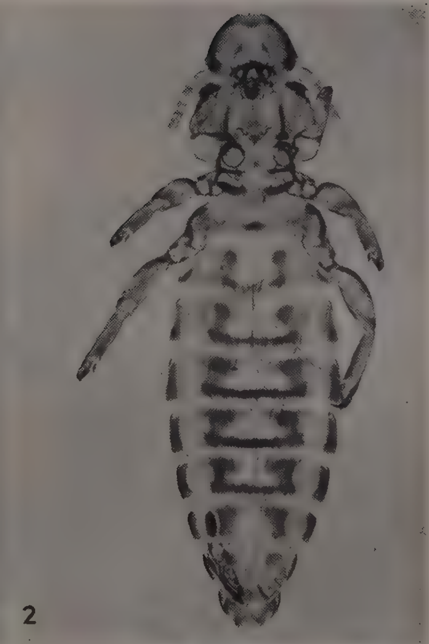
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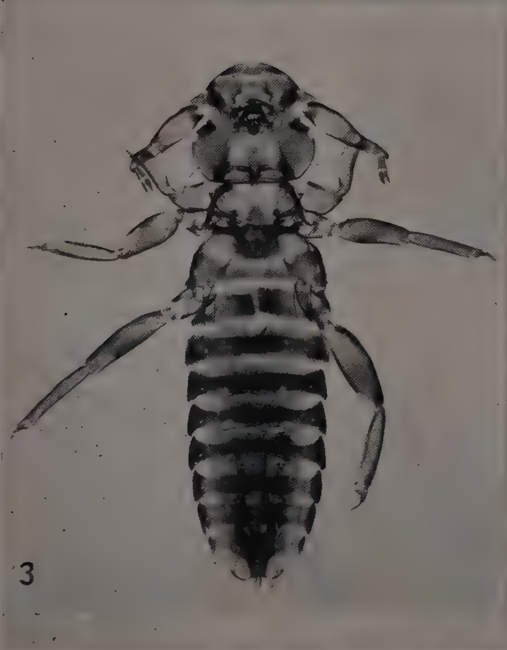
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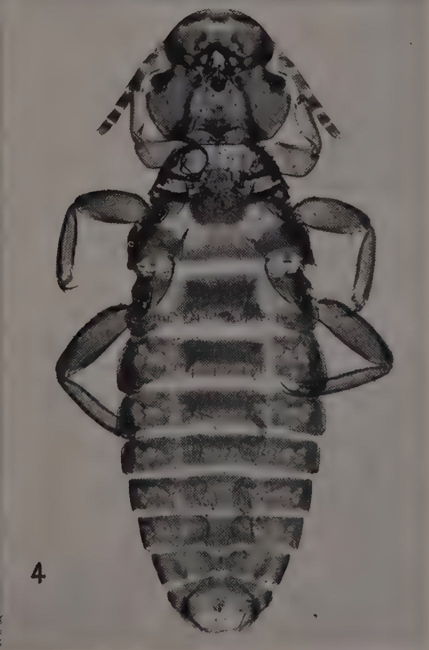
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FIG. 1.—*Colilipeurus r. radiatus* (Neumann). ♂ × 60.
FIG. 2.—*Colilipeurus r. radiatus* (Neumann). ♀ × 40.
FIG. 3.—*Falcolius jordani* sp. n. ♂ × 40.
FIG. 4.—*Falcolius jordani* sp. n. ♀ × 40.

T. Clay. Photographs by M. G. Sawyers.

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A KEY TO THE AFRICAN GENERA OF LYMANTRIIDAE (LEPIDOPTERA).

By C. L. Collenette.

I am glad to have the opportunity of contributing the following paper to the Jubilee Volume in honour of Dr. Karl Jordan, in gratitude for his assistance and encouragement in the year 1928, when I first commenced the study of the family Lymantriidae.

The paper is mainly a result of a study of the Lymantriidae in the collection of the British Museum (Nat. Hist.). Previous keys were without exception composed many years ago, with a much smaller number of genera, and too often a genus was included on the examination of one out of several species or even of only one specimen. The present key contains 91 genera, of which only 66 were included in the Ethiopian section of Seitz, *Grossschmett. Erde*, Vol. 14, 1926–27.

Previous keys which have afforded me the most help are:

Aurivillius, C., 1904, Übersicht der Gattungen der Äthiopischen Lymantriiden. *Ark. Zool.* **2** (4): 62. (With 35 genera, of which a number are no longer in use).

Hampson, Sir G. F., 1905, The Moths of South Africa. *Ann. S. Afr. Mus.* (3) **9** : 390.

Janse, A. T. J., 1915, Contribution towards our Knowledge of the South African Lymantriidae. *Ann. Transv. Mus.* **5** : 3.

Although the best single guide to relationship in the family is in the form of the male genitalia I have not used this character in the key, but have employed such as can readily be seen with a hand lens.

I have also made no use of the process on the fore tibia, illustrated by Janse in his excellent plates, as it is difficult to examine in detail without special preparations. The palpi have been avoided where possible, as they are not readily described in a key and do not usually show marked generic differences.

A character which appears to be completely reliable is the number of pairs of spurs on the hind tibia, but great care must be taken not to confuse those on the middle leg with those on the hind leg, as has frequently been done even in descriptions of new genera.

The presence or absence of an areole in the fore wing is a distinction which has been used by all authors, being easy to see and convenient. However, it has been a frequent cause of failure in a key, as a single species often has areolate and inareolate specimens, a single insect sometimes being asymmetrical in this respect. Where exceptional specimens amount to less than some 10 per cent. of the whole, I have ignored them, but in the case of seven genera where the exceptions are common these have been included in two places in the key. The same considerations apply to genera distinguished partly by the separation or stalking of a pair of veins and for this reason, where more than one specimen of the same species is available when using the key, it is sometimes advisable to check the venation of one with another.

Finally, a very useful distinction in many genera is the presence or absence of markings or of more than one colour on the upper side and fringe of the hind wing, but here again a few genera appear in both categories and have been placed under each in the key.

I have been tempted to suggest an order in which the genera might be arranged phylogenetically. The order employed in the collection of the British Museum (Nat. Hist.) at the last re-arrangement of the African Lymantriidae was founded on that used by Dr. Hering in Seitz, but, as specimens and new genera accumulated, very many alterations have been made. A phylogenetic key should evaluate and take into consideration a number of different characters, one of the most important being those deriving from the early stages. The ova, larvae and pupae of the African Lymantriidae are fully known in extremely few species, but are now being increasingly studied. I feel that little is to be gained in a present attempt to place the genera in a natural order, and moreover that a table founded on our present knowledge would be quickly out of date.

Resulting from the compilation of the key and from notes made previously, certain corrections have been made in the genera, as follows :

(1) (*Aclonophlebia* Butler, 1898)=*Rhypopteryx* Aurivillius, 1879. The latter genus is represented in the British Museum collection by a short series of females of the type species *R. sordida* Aurivillius. In the description of the male and a careful comparison of the female, no generic distinction can be found from the well known genus *Aclonophlebia*, and this name must unfortunately sink. A further species shown in this genus in Seitz, *Rhypopteryx summisa* Hering, 1927, is a *Stracena*, closely allied to *S. promelaena* Holland, 1893.

(2) (*Bicelluphora* Janse, 1915) = *Dasychira* Hübner, 1809. *Bicelluphora*, with type *B. argentea* Janse, 1915, was described from a single male, in which vein 11 anastomoses with the stalk of 9 and 10 to form a second areole. *B. argentea* is synonymous with *Dasychira octophora* Hampson, 1905, and of the 12 males in the British Museum collection, a single specimen has an abnormal vein 11 almost matching Janse's type. *D. octophora* is correctly placed in *Dasychira*, and *Bicelluphora* is accordingly sunk.

(3) (*Liparodonta* Hering, 1927) = *Euproctidion* Holland, 1893. By courtesy of Dr. Martin Hering, I have examined the unique type, *L. convexa* Hering, from the Berlin Museum. This insect has the venation of *Euproctidion*, dorsal crests of hair scales with spatulate tips, and similar upstanding hair scales on fore and middle legs. There is a small patch of brownish red at the anal angle of upper side of hind wing. The second species in the genus, *Liparodonta uniformis* Hering, 1927, has also been transferred to *Euproctidion*.

(4) (*Lymantica* Collenette, 1926) =*Lymantria* Hübner, 1820. The type of the genus, *Lymantica epelytes* Collenette, may be an aberrant specimen of *Lymantria atala* Swinhoe, 1923, but only a single female of each is known. The genitalia show close similarity.

(5) *Pachycispia* Butler, 1882, type *P. picta* Butler, 1882. The type species has vein 5 in both wings originating from above the centre of the cross vein, and in other respects, notably in the antennae, is plainly a Notodontid. The genus is therefore transferred and placed next to *Trotonotus* Butler and *Paratrotonotus* Aurivillius.

(6) *Pseudarctia* Bethune-Baker, 1911, type *P. nivea* Bethune-Baker, 1911. This common species, which has a considerable proboscis, has been compared with *Spilosoma habrotima* Tams, 1930, to which it is clearly related in structure

and appearance. The genus *Pseudarctia* is now sunk to *Spilosoma* Curtis, 1825, (Arctiinae) and *P. nivea* transferred to that genus.

In common with Janse, (1915, *Ann Trans. Mus.* **5** : 28), I have found it most difficult to separate the genus *Laelia* from *Dasychira* on external characters only. The two seem to be rather closely allied, but are best retained as separate genera, and I agree with Janse that the palpi afford the most reliable character.

It has been found necessary to erect a new genus for *Aroa lata* Holland, 1893, see clause 21 in the key and the description which follows. This species, known only in the female sex, has points of resemblance to species of the genera *Lymantria*, *Imaus* and *Cispia*, but is excluded from all by having only one pair of spurs on the hind tibia.

Usimbara gen. n.

Female.—Proboscis short and aborted. Palpus upturned, the third segment one-third the length of second. Eye elliptical, greatest length about the width of frons. Antenna bipectinate, one-third the length of costa. Abdomen two-thirds the length of inner margin of hind wing. Legs rather sparsely haired ; process on fore tibia stout, curved at tip and slightly longer than tibia ; mid and hind tibiae with a single pair of stout, rather long spurs. Costa and inner margin of fore wing moderately rounded, termen almost straight ; vein 12 almost parallel with costa, 11 from cell at three-quarters, 10 to 7 stalked, with 10 from two-thirds total length of stalk, 9 and 8 separating at three-quarters length of stalk, 7 from just above upper angle of cell, 6 from well below upper angle, 5 from well above lower angle of cell, 4 from lower angle, 3 from twice the distance from 4 that 4 is from 5, 2 from two-thirds lower margin of cell, anal vein simple at base. Hind wing with costa and inner margin almost straight, termen distinctly angled at veins 3 and 4 ; vein 8 anastomosing with cell for a short distance at one-third of cell, 7 and 6 on a short stalk, 5 and 4 well separated, 3 from slightly further from 4 than 4 from 5, 3 from two-thirds lower margin, anal veins present. Frenulum present.

Gender : Feminine. Type species : *Aroa lata* Holland, 1893.

Key to the African Genera of Lymantriidae.

1		Female apterous	2
		Female brachypterous or fully winged, male fully winged . .	3
2	(1)	Range north and south Africa	**Bracharoa** Hampson
		Range west, central and east Africa . . .	**Orgyia mixta** Snellen
3	(1)	One pair of spurs on hind tibia	4
		Two pairs of spurs on hind tibia	48
4	(3)	Areole absent in fore wing	5
		Areole present in fore wing	30
5	(4)	Vein 11 arising from cell and not anastomosing with 12 . . .	6
		Vein 11 arising from cell and anastomosing with 12, or absent .	29
6	(5)	Veins 3 and 4 of hind wing stalked	7
		Veins 3, 4 and 5 of hind wing all separate, 3 and 4 occasionally from a point	8
7	(6)	Vein 5 in both wings rather indistinct, straight, and rising almost midway between veins 4 and 6 ; Madagascar only	**Dasychoproctis** Hering
		Vein 5 in both wings rising nearer to 4 than to 6; not found in Madagascar	**Pyrrhopteryx** Hering
8	(6)	Veins 6 and 7 of hind wing stalked, occasionally from a point .	9
		Veins 6 and 7 of hind wing unstalked, occasionally from a point	22

9 (8) Vein 8 of hind wing fused for long distance with cell 10
Vein 8 of hind wing fused for short distance or only touching or approaching cell 11

10 (9) Vein 10 of fore wing from cell; all veins of fore wing present **Homoeomeria** Wallengren
Vein 10 of fore wing stalked with 7/9; all veins of fore wing present . . . . **Synogdoa** Aurivillius
Veins 7 and 10 of fore wing absent; two pairs of thin dorsal tufts on basal segments of abdomen . . **Paraproctis** Bethune-Baker
Vein 7 of fore wing absent; no dorsal tufts **Carpenterella** Collenette
Vein 8 and 9 of fore wing fused . . . . . **Theriophila** Hering

11 (9) Vein 10 of fore wing absent 12
Vein 7 of fore wing and 3 of hind wing absent; discocellulars of both wings absent . . . . **Micraroa** Hampson
The above veins present 13

12 (11) A black spot at centre of inner margin of hind wing; frenulum present . . . . **Pseudogenusa** Rebel
No such spot; frenulum absent . . . . **Pseudostracilla** Hering

13 (11) Outer angle of hind wing produced to a pronounced point **Leptepilepta** Collenette
Outer angle of normal shape 14

14 (13) Vein 10 of fore wing from cell 15
Vein 10 of fore wing from stalk 20

15 (14) Discocellulars of fore wing with dark border, crescent-shaped **Naroma** Walker
Discocellulars of fore wing unmarked, or with one or two spots or a single streak 16

16 (15) Veins of fore wing prominent and darker than ground colour . 17
Veins of fore wing not distinct or darker than ground colour . 18

17 (16) Vein 3 of fore wing straight . . . **Parapirga** Bethune-Baker
Vein 3 of fore wing distinctly curved . . . **Stilpnaroma** Hering

18 (16) Fore wing with dull, non-reflecting surface; wings unmarked or fore wing with a single dark spot between the origins of veins 2 and 3, a double spot on the discocellulars or costa edged with black basally . . . . **Olapa** Walker
Fore wing with gleaming reflecting surface; wings unmarked or with a single dark marking on the discocellulars or dark edging to costa 19

19 (18) Pectinations of antenna not markedly plumose; wings unmarked or with a single spot on the discocellulars of fore wing or costa edged with black . . . . **Leucoma** Stephens
Pectinations of antenna separate and bushy, especially in the male; wings unmarked . . . . **Pteredoa** Hampson

20 (14) Hind wing black . . . . **Stenaroa** Hampson
Hind wing bright orange or yellow, with black terminal border **Barlowia** Talbot
Hind wing not as above 21

21 (20) Hind wing distinctly angled at veins 3 to 4 **Usimbara** gen. n.
Hind wing of normal shape . . . . **Stracena** Swinhoe

22 (8) Vein 10 of fore wing from cell 23
Vein 10 of fore wing from stalk of 7 to 9 24

23 (22) Discocellulars of fore wing with dark border, crescent-shaped **Naroma** Walker
No dark border or mark on discocellulars . . . **Leucoma** Stephens

24	(22)	Wings semi-hyaline	25
		Wings opaque	26
25	(24)	Discocellulars of fore wing sharply right-angled at centre, with traces of a median vein in the cell	**Stracilla** Swinhoe
		Discocellulars of fore wing not strongly angled	**Hyaloperina** Aurivillius
26	(24)	Vein 3 of hind wing originating nearer to 4 than 4 from 5, occasionally equidistant; abdomen of female pointed and ovipositor usually protruding	27
		Vein 3 of hind wing originating further from 4 than 4 from 5, occasionally equidistant; abdomen of female blunt and ovipositor not visible	28
27	(26)	Abdomen stout, with bushy, upstanding hairs on thorax	**Polymona** Walker
		Abdomen rather slender, with close-set hairs on thorax	**Rhypopteryx** Aurivillius (*Aclonophlebia* Butler)
28	(26)	Vein 6 of fore wing from far below the angle, originating about half-way between angle and median fold	**Eala** Collenette
		Vein 6 of fore wing from angle or not far below	**Stracena** Swinhoe
29	(5)	Vein 11 of fore wing arising from cell and anastomosing with 12	**Leucoperina** Aurivillius
		Vein 11 of fore wing absent; 10 from stalk	**Opoboa** Tessmann
		Vein 11 absent, 10 from cell	**Leucoma** Stephens
30	(4)	Veins 6 and 7 in hind wing unstalked	31
		Veins 6 and 7 in hind wing stalked or completely fused	32
31	(30)	Apical area of fore wing, to discocellulars and vein 6, darkened	**Cimola** Walker
		Apical area of fore wing uncoloured	**Stracilla** Aurivillius
32	(30)	Veins 3 and 4 in hind wing stalked, 5 unstalked	33
		Veins 3 to 5 in hind wing unstalked	34
33	(32)	Hind wing light coloured, female fully winged	**Argyrostagma** Aurivillius
		Hind wing dark brown in male; female brachypterous with hind wing light-coloured	**Orgyia hopkinsi** Collenette
34	(32)	Veins 4 and 5 of fore wing stalked	35
		Veins 4 and 5 of fore wing unstalked	37
35	(34)	Fore wing without fasciae	**Bracharoa** Hampson
		Fore wing with fasciae	36
36	(35)	Hind wing drab	**Orithrepta** Collenette
		Hind wing orange with broad dark border	**Orgyia tricolor** Herrich-Schäffer
37	(34)	Vein 11 arising from areole	38
		Vein 11 arising from cell	40
38	(37)	Apical area of fore wing uncoloured	**Lepidopalpus** Janse
		Apical area of fore wing coloured	39
39	(38)	In both wings, posterior margin of cell greatly produced distally to meet veins 4 and 5	**Anexotamos** Hering
		In both wings, posterior margin of cell of normal shape	**Somatoxena** Aurivillius
40	(37)	Hind wing with anal angle produced to a pronounced point	**Leptepilepta** Collenette
		Hind wing of normal shape	41
41	(40)	Apical area of fore wing, and usually the distal third or half of both wings, dark, the remaining area of both wings whitish	**Pirga** Aurivillius

Wings not so coloured 42

42 (41) Fore wing marked with one or more fasciae 43

Wings without fasciae, ground colour white or pale 44

43 (42) Ground colour dark brown or white; expanse not exceeding ♂ 40 mm., ♀ 50 mm. . . . . **Orgyia** Ochsenheimer

Ground colour of hind wing usually yellow; expanse exceeding ♂ 50 mm., ♀ 55 mm. . . . . **Ogoa** Walker

44 (42) Veins of fore wing distinctly prominent and darker than ground colour 45

Veins of fore wing not as above 46

45 (44) Vein 3 of fore wing straight . . . . . **Parapirga** Bethune-Baker

Vein 3 of fore wing distinctly curved . . . **Stilpnaroma** Hering

46 (44) Frenulum present; not occurring in Madagascar . **Olapa** Walker

Frenulum absent 47

47 (46) Expanse under 50 mm.; body and wings entirely white or with black edging at base of costa and small spots at apex and tornus **Pirgula** Tessmann

Expanse over 50 mm.; body and wings entirely white or with a series of subterminal spots interneurally in fore wing; occurring only in Madagascar . . . . **Eopirga** Hering

48 (3) Areole absent in fore wing 49

Areole present in fore wing 80

49 (48) Vein 11 in fore wing free and arising from cell 50

Vein 11 arising from cell, ascending sharply and anastomosing with or touching 12 for a short distance, or joined by a bar **Lymantria** Hübner

50 (49) Hind wing on upper side with markings, or colour contrasting strongly with colour of fringe 51

Hind wing on upper side without markings, and not contrasting strongly with colour of fringe 66

51 (50) Veins 3 and 4 of hind wing stalked 52

Veins 3 and 4 of hind wing separate or not both present . . 55

52 (51) Vein 8 of hind wing fused with cell and separating shortly before end of cell; veins 8 and 9 of fore wing entirely fused; wings predominately orange . . . . **Chrysocyma** Hampson

Not having these features 53

53 (52) Hind wing unmarked, not yellow in colour **Lymantriades** Bethune-Baker

Hind wing with markings, or if unmarked then yellow in colour 54

54 (53) Hind wing having a dark postmedial fascia parallel with the termen; wings rather narrow . . . . . . **Tearosoma** Felder

No fascia in this position, wings rather broad . . . **Aroa** Walker

55 (51) Veins 6 and 7 of hind wing stalked 56

Veins 6 and 7 of hind wing unstalked 60

56 (55) Vein 4 of hind wing absent . . . . . . **Porthesaroa** Hering

Vein 4 of hind wing present 57

57 (56) Ground colour of wings orange or yellowish, veins of both wings darker than ground colour. . . . . . **Pseudobazisa** Bryk

Not having both these characters 58

58 (57) Hind wing on upper side whitish, with a faint darkening in apical area; expanse exceeding 45 mm. . . . . **Sycnacedes** Collenette

Not having both these characters 59

59 (58) Hind wing uniform light brown, with a dark streak on the discocellulars and a dark subterminal fascia. South Africa only **Cymaroa** Hampson

Not having all these characters . . . . **Aroa** Walker

60 (55) Expanse at least 70 mm.; wings with a series of conspicuous interneural subterminal white spots . . . . **Otroeda** Walker

Not having both these characters 61

61 (60) Termen of fore wing towards apex slightly convex, resulting in a sharp angle inwards at vein 8 . . . . **Heteronygmia** Holland

Termen normally rounded 62

62 (61) Occurring only in Madagascar . . . . . **Numenoides** Butler

Not occurring in Madagascar 63

63 (62) Ground colour of wings orange or yellowish, veins of both wings darker than ground colour. . . . . . . **Pseudobazisa** Bryk

Not having both these characters 64

64 (63) Hind wing uniform light brown, with a dark streak on the discocellulars and a dark subterminal fascia. South Africa only **Cymaroa** Hampson

Not having all these characters 65

65 (64) Vein 3 of fore wing originating further from 4 than 4 from 5; abdomen usually tinged with pink or red; female with pointed abdomen and protruding ovipositor . . . **Palasea** Wallengren

Vein 3 of fore wing originating nearer to 4 than 4 from 5, or occasionally equidistant; abdomen never tinged with pink or red; female with ovipositor not protruding . . **Aroa** Walker

66 (50) Veins 3 and 4 or 4 and 5 of hind wing stalked, or from a point. (One vein may be absent) 67

These veins all separate. (One vein may be absent) . . . 74

67 (66) Vein 8 in hind wing fused with cell and separating shortly before end of cell; veins 8 and 9 of fore wing entirely fused; wings predominantely orange . . . . **Chrysocyma** Hampson

Not having all these characters 68

68 (67) Veins 6 and 7 of hind wing on a stalk of one-half; the only markings on fore wing a black spot on the discocellulars and a postmedial fascia formed of a single line . . . **Neoliparina** Schultze

Not having all these characters 69

69 (68) Occurring in Madagascar only; vein 4 of hind wing absent; veins 4 and 5 of fore wing stalked; fore wing with brown markings on a ground colour of white . . **Noliproctis** Hering

Not having all these characters 70

70 (69) An easily seen raised circular process on the frons between the eyes, bare of scales; expanse not exceeding 35 mm. **Laelioproctis** Hering

Not having these characters 71

71 (70) Abdomen dorsally orange with fuscous marking at each segment; fore wing brown with well-defined antemedial and postmedial fasciae . . . . **Lymantriades** Bethune-Baker

Not having these characters 72

72 (71) Occurring in Madagascar only; expanse not exceeding 20 mm.; fore wing with a series of preterminal interneural brown spots; a brown line terminally, broken at the veins . **Suarezia** Hering

Not having all these characters 73

73 (72) Abdomen with dorsal tufts on first three segments; fore wing brown with several crenulated fasciae; fore leg very hairy **Homochira** Hampson

Not having all these characters . . . . . . **Euproctis** Hübner

74 (66) Veins 6 and 7 of hind wing stalked 75

Veins 6 and 7 of hind wing unstalked 79

75 (74) Occurring in Madagascar only; colour of fore wing dragon's-blood red; a conspicuous white patagium in the male **Perinetia** Collenette

Not having all these characters 76

76 (75) Fore wing with ground colour yellow, covered with large interneural orange spots, and with a curved black streak on the proximal side of the discocellulars; expanse exceeding 40 mm. **Mylantria** Aurivillius

Not having all these characters 77

77 (76) Occurring in Madagascar only; expanse over 45 mm.; no yellow on wings . . . . **Sycnacedes** Collenette

Not having all these characters 78

78 (77) Vein 4 of hind wing absent, and with preterminal and terminal markings on fore wing . . . . **Porthesaroa** Hering

Vein 4 of hind wing present, or, if absent, no preterminal and terminal markings on fore wing and with hind wing white or pale cream . . . . **Euproctis** Hübner

79 (74) Termen of fore wing towards apex slightly convex, resulting in a sharp angle inwards at vein 8 . . . . **Heteronygmia** Holland

Termen not having this feature . . . . . . **Palasea** Wallengren

80 (48) Vein 11 of fore wing arising from areole 81

Vein 11 of fore wing arising from cell 82

81 (80) Veins 3 and 4 of hind wing stalked . . . . **Lacipa** Walker

Veins 3 and 4 of hind wing separate . . . **Lepidolacipa** Hering

82 (80) Fore wing with a series of regular postmedial or subterminal interneural spots, occasionally obsolescent; palpi porrect and easily visible from above, vertical aspect; third segment rather bare, with adpressed hair . . . . . **Laelia** Stephens

Not having these characters 83

83 (82) Areole very long; apical half of wing fuscous 84

Areole of normal length 85

84 (83) Vein 8 of hind wing connected with cell for half the length of cell **Marbla** Swinhoe

Vein 8 of hind wing connected with cell near base only **Paramarbla** Collenette

85 (83) Hind wing unmarked 86

Hind wing with markings or with fringes differently coloured . 109

86 (85) In hind wing, veins 3 to 5 unstalked, 6 and 7 unstalked . . 87

In hind wing, veins 3 to 5 unstalked, 6 and 7 stalked . . . 90

In hind wing, veins 3 and 4 stalked, 6 and 7 stalked . . . 103

87 (86) Termen of fore wing with a pointed projection at or just below vein 4 . . . . **Lomodonta** Holland

Termen of fore wing without a pointed projection 88

88 (87) Fore wing unmarked or with a small spot on discocellulars or with veins darker than ground colour . . . . . **Cropera** Walker

Fore wing with fasciae and/or spots 89

89 (88) Abdomen with dorsal crests of hair-scales with spatulate tips and similar upstanding hair-scales on fore and middle legs, sometimes worn off on abdomen . . . . **Euproctidion** Holland

No dorsal crests or spatulate hair-scales on abdomen or legs **Euproctoides** Bethune-Baker

90 (86) Vein 3 of hind wing arising nearer to 4 than 4 from 5 . . . 91

Vein 3 of hind wing arising further from 4 than 4 from 5 . . 95

91 (90) Costal area of fore wing lighter than inner marginal area, the division between the two clearly marked and reaching from termen to base of wing . . . . **Psalis** Hübner

Fore wing not so marked 92

92 (91) Fore wing sharply angled or even pointed at apex and usually with an isolated dark marking on the discocellulars **Conigephyra** Collenette

Not having these characters 93

93 (92) Insect lightly built with wings semi or slightly transparent and with markings on fore wing simple or absent **Marblepsis** Hering

Insect more heavily built, wings opaque, fore wing well marked 94

94 (93) Abdomen with dorsal crests of hair scales with spatulate tips and similar upstanding hair scales on fore and middle legs, sometimes worn off on abdomen . . . **Terphothrix** Holland

Crests and groups of hair scales either not present or without spatulate tips . . . . **Dasychira** Stephens

95 (90) Veins of fore wing outlined with coral red and a conspicuous almost straight fuscous postmedial fascia from costa to inner margin . . . . **Thambeta** Collenette

Not having these characters 96

96 (95) Each pectination of antenna fuscous in basal quarter, contrasting strongly with pale distal portion . . . **Creagra** Wallengren

Not having this character 97

97 (96) Vein 8 of hind wing separated from cell, sometimes joined to it by a bar 98

Vein 8 of hind wing touching or anastomosing with cell . . . 101

98 (97) Fore wing entirely white, or edged with black at base of costa **Croremopsis** Hering

Not having these characters 99

99 (98) Fore wing with at least two interneural spots, sometimes numerous and in the form of a fascia . . . . . . **Crorema** Walker

Fore wing without spots, or with a single spot on discocellulars 100

100 (99) Antennal shaft black or very dark . . . . **Ruanda** Strand

Antennal shaft yellow, light brown or whitish . **Cropera** Walker

101 (97) Veins 7 and 10 arising from areole and usually approximately opposite . . . . **Marblepsis** Hering

One or both of these veins arising well beyond the end of areole 102

102 (101) Fore wing sharply angled or even pointed at apex and usually with an isolated dark marking on the discocellulars **Conigephyra** Collenette

Not as above, and with veins conspicuously darker than ground colour . . . . **Ruanda** Strand

103 (86) Costal area of fore wing lighter than inner marginal area, the division between the two clearly marked and reaching from termen to base of wing . . . . **Psalis** Hübner

Forewing not so marked 104

104 (103) Termen slightly convex from vein 4 to vein 7 and with two dark markings in terminal area, at veins 2–3 and 5–6 **Jacksonia** Collenette

Not having these characters 105

105 (104) Fore wing with three prominent white markings on an unmarked dark ground, including a double line in the terminal area, curving round to base of vein 2, and a large wedge-shaped mark with apex at lower angle of cell . . . . **Neomardara** Hering

Not having these characters 106

106 (105) Expanse not exceeding 40 mm.; fore wing having at least some orange markings on a light ground, apex rather pointed **Lacipa** Walker

Not having these characters 107

107 (106) Fore wing long and narrow, the only prominent marking a dark patch or spot on the discocellulars; expanse not exceeding ♂ 40 mm., ♀ 45 mm. . . . . **Casama** Walker

Not having these characters 108

108 (107) Fore wing narrow and apex pointed, especially in male; fasciae and other markings present; not occurring in Madagascar **Hemerophanes** Collenette

Apex of fore wing of normal shape . . . . **Dasychira** Stephens

109 (85) In hind wing, veins 3 to 5 unstalked, 6 and 7 unstalked . . 110

In hind wing, veins 3 to 5 unstalked, 6 and 7 stalked . . . 115

In hind wing, veins 3 and 4 stalked, 6 and 7 stalked 126

110 (109) Pectinations of antenna black or dark and veins of both wings notably darker than ground colour 111

Not having both these characters 112

111 (110) Ground colour of wings orange or yellowish; apical and terminal areas and fringes dark in male . . . . **Pseudobazisa** Bryk

Not as above excepting for a narrow but distinct dark terminal line in both sexes . . . . **Cadurca** Swinhoe

112 (110) Fore wing unmarked, or with a small spot on discocellulars, or with veins darker than ground colour . . . **Cropera** Walker

Fore wing with a pattern of fasciae and/or spots 113

113 (112) Termen of fore wing produced to a point at or just below vein 4 **Lomadonta** Holland

Termen of fore wing without a pointed projection 114

114 (113) Abdomen with dorsal crests of hair-scales with spatulate tips and with similar upstanding hair-scales on fore and middle legs, sometimes worn off on abdomen . . . . **Euproctidion** Holland

No dorsal crests or spatulate hair-scales on abdomen or legs **Euproctoides** Bethune-Baker

115 (109) Termen of fore wing with two main projections just below veins 4 and 7 respectively; expanse over 60 mm. . . **Barobata** Karsch

Not having both these characters 116

116 (115) Wings semi-hyaline; hind wing with a small black spot at the termination of each vein . . . . . **Scaphocera** Saalmüller

Not having these characters 117

117 (116) Abdomen with dorsal crests of hair-scales with spatulate tips and similar upstanding hair-scales on fore and middle legs, sometimes worn off on abdomen . . . . **Terphothrix** Holland

Crests and groups of hair-scales either not present or without spatulate tips 118

118 (117) An oval patch of white in centre of hind wing, with clear-cut edges, and occupying one-third of the wing area; expanse over 55 mm. . . . . **Abynotha** Swinhoe

Not having all these characters 119

119 (118) Wings opaque; a single black spot on discocellulars of both wings and a further spot near base of fore wing **Sphragista** Collenette

Not having all these characters 120

120 (119) Wings opaque, white, with veins of fore wing 1c, 4, 6 to 8 and costa outlined prominently with black . . **Grammoa** Aurivillius

Not having all these characters 121

121 (120) Fore wing sharply angled or even pointed at apex and usually with an isolated dark marking on the discocellulars **Conigephyra** Collenette

Not having these characters 122

122 (121) Ground colour of wings orange or yellowish ; apical and terminal areas and fringes dark in male. . . **Pseudobazisa** Bryk

Not having all these characters 123

123 (122) Fore wing with pattern of spots and/or fasciae **Dasychira** Stephens

Fore wing either unmarked or with a single mark on the discocellulars and/or veins darker than ground colour ; occasionally slight dark shading in the apical area 124

124 (123) Shaft and pectinations of antenna yellow, light brown or whitish **Cropera** Walker

Pectinations of antenna black or very dark, shaft usually the same 125

125 (124) Veins of fore wing prominently darker than ground colour, but those of hind wing, except occasionally in terminal area, not darker . . . . **Ruanda** Strand

Veins of both wings prominently darker than ground colour **Cadurca** Swinhoe

126 (109) Expanse not exceeding 25 mm. ; wings dark and unmarked, but with yellow fringes and/or margins . . . **Laelaroa** Hering

Not having these characters 127

127 (126) Fore wing with three prominent white markings on an unmarked dark ground, including a double line in the terminal area, curving round to the base of vein 2, and a large wedge-shaped mark with apex at lower angle of cell . . **Neomardara** Hering

Not having these characters 128

128 (127) Expanse not exceeding 45 mm. ; fore wing having at least some orange markings on a light ground, apex rather pointed **Lacipa** Walker

Not having all these characters 129

129 (128) Fore wing narrow and apex pointed, especially in male ; not occurring in Madagascar . . . . . . **Hemerophanes** Collenette

Apex of fore wing of normal shape . . . . **Dasychira** Stephens

" On closer investigation the genus [*Utetheisa*, Lepid. : Arctiidae] proves nevertheless to be a bundle of contradictions which obscure the real relationship of the species with one another and have led the systematists astray in their attempt to group the species in a natural order. But putting the counters into their right places is only the beginning of a game. The species have arisen from a common basis, each species representing the ancestor in a specially modified form. The differences acquired and the similarities retained are facts before us that ask for an enquiry into their meaning."

(Jordan, K., 1939, *Novit. zool.* **41** : 251.)

" The [as yet unknown] male of this species [*galapagensis*] should, therefore, be expected to have longer pectinations than any other *Utetheisa*, if evolution were bound to follow the demands of human logic. However, it is better to be agnostic when dealing with nature. Prophesies are only quite safe if the wording is sufficiently ambiguous."

(Jordan, K., 1939, *Novit. zool.* **41** : 261.)

A NOTE ON A PECULIAR ABDOMINAL ORGAN IN CERTAIN TORTRICIDAE (LEPIDOPTERA).

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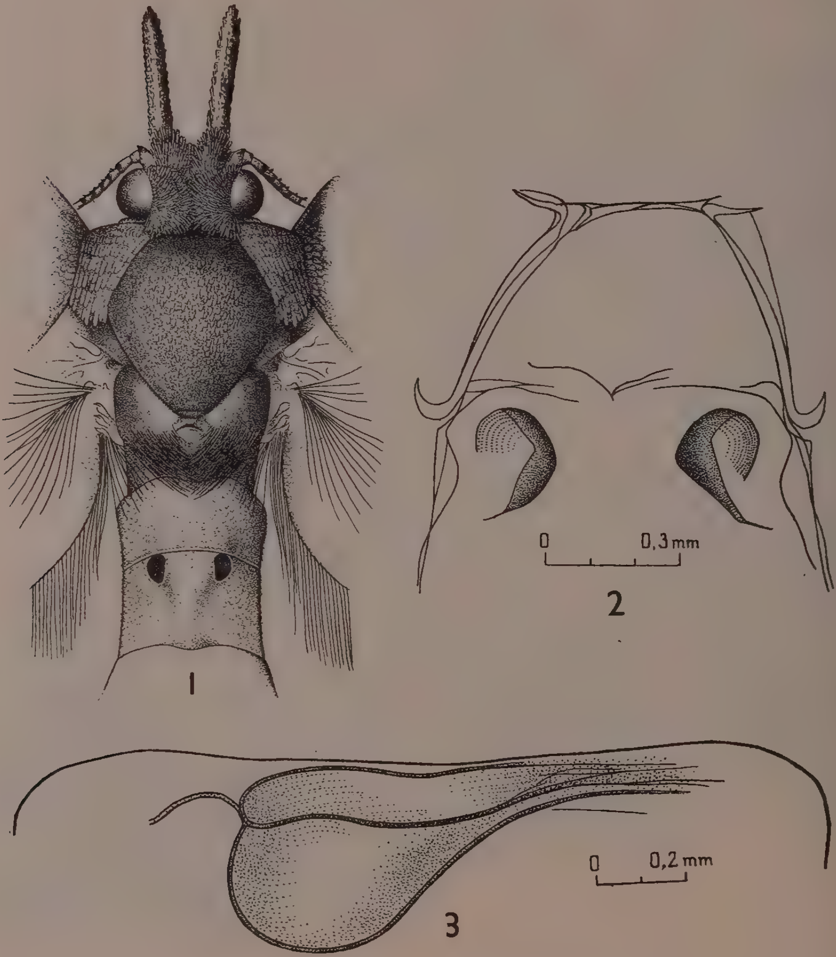
With 1 Plate and 3 Text-figures.

When studying the Microlepidoptera collected during the Third Archbold Expedition to New Guinea in 1938–1939, I discovered a genus of Tortricidae with a new, striking structure, viz., a pair of holes in the abdomen. In the first specimen that came to my notice I assumed these holes to be due to damage caused by some adephagous insect, but before long the symmetrical position of the openings made me realise that they were natural. This peculiar feature appeared to be characteristic of the new genus, which belongs to the tribe Cnephasiini of the subfamily Tortricinae, and which I called *Tremophora* (τρῆμα = a hole, φέρω = to bear). It is so far represented by five species from the Snow Mountains in Central Dutch New Guinea (1953), viz., *T. scintillans* Diakonoff, *carycina* Diakonoff, *alopex* Diakonoff, *guttulosa* Diakonoff, and *coniortus* Diakonoff, and by a sixth species, *microplecta* Diakonoff, that became known to me later from the mountains of Papua in Australian New Guinea (1953*a*).

The genus *Tremophora* differs from all its allies, and, as far as I know, also from all other Lepidoptera, in possessing the above mentioned peculiar organ in the tergite of the second abdominal segment. It consists of a paired, rather deep excavation of the segment, externally having the appearance of two rather large, somewhat kidney-shaped holes with slightly elevated edges, situated towards the anterior edge of that segment, with their long axis directed longitudinally (fig. 1). The excavations penetrate downwards and slightly forwards (figs. 2 and 3), each forming a short blind tunnel with a thick, sclerotised, and apparently smooth wall. These organs, which I called the "dorsal organs", are present and are equally developed in both sexes; their superficial appearance is similar in the six known species of *Tremophora*.

The available material is so scanty that, unfortunately, it does not enable the function of these organs to be ascertained. It is hardly appropriate for anatomical study and not suitable for a histological study. The few available desiccated abdomina were immersed in water for a long time to restore them to a more natural shape, and were sectioned afterwards with a microtome. As might be expected, the results were disappointing. No traces of neural elements could be found in the sections; neither did the structure of the sclerotised walls of the cavities provide any indication as to the function of the dorsal organs.

At first I considered the possibility of these organs being a kind of tympanal organ of peculiar construction. It is well known that tympanal organs, which may have auditory function, occur in two forms, viz., thoracic, situated in the pleural region of the metathorax, and abdominal, in the lateral region of the first abdominal segment. Some twelve Lepidopterous families of the Phalaenid relationship possess thoracic tympanal organs, while the organs of the abdominal kind are found in some seven families of the Geometrid group. The remaining Lepidoptera, including the Microlepidoptera *sensu stricto* (excluding the Pyralidoidea), have no tympanal organs at all. The presence or absence of these organs is of paramount importance in the taxonomy of the Lepidoptera.



Figs. 1–3.—(1) *Tremophora carycina* Diakonoff. Male, dorsal aspect of head, thorax and the base of the abdomen with the dorsal organs (14 ×). (2) *T. coniortus* Diakonoff. Female, dorsal aspect of the base of the abdomen, after maceration with 10% potassium hydroxyde. Walls of the cavities punctuated (slide no. 479). (3) *T. alopex* Diakonoff. Female, dorso-lateral aspect of the right cavity of the dorsal organ, after maceration with 10% potassium hydroxyde (slide no. 474a).

By their position alone the dorsal organs are quite different from the known tympanal organs which are otherwise always situated laterally. Furthermore, I have not been able to detect any structures that might represent the tympanum or tympanal membrane itself, which is a characteristic of this kind of organ. The inner surface of the dorsal organs is smooth and apparently of even thickness throughout (Pl. 1), without any indication of the presence of a membranous portion.

The dorsal organs might be scent organs. These latter organs, however, are usually found only in one sex. Where they occur in both sexes they are usually differently built in the male and in the female, always considerably adding to the sexual dimorphy. The dorsal organs of *Tremophora*, however, are exactly alike in the males and the females, which rules out their interpretation as scent organs.

It was suggested to me that the dorsal organs might be the equivalents of the so-called mite chambers of certain Hymenoptera (e.g., *Xylocopa*, *Mesotrichia*), cavities of the body of special structure, inhabited by peculiarly specialised Acari. However, I have never observed any trace of mites in these organs ; moreover, mite chambers have never yet been recorded in Lepidoptera.

Whatever function the dorsal organs may serve, their isolated occurrence in a single genus of Lepidoptera is extremely puzzling. The problem of their true character can only be solved after an anatomical and a histological study of either fresh material, or of material suitably preserved, e.g., in alcoholic Bouin's fluid. The hope that such material of *Tremophora* or of allied, so far undiscovered, forms, will soon become available, is, alas, very small. I therefore decided to publish this note, though I am well aware of its incompleteness.

ACKNOWLEDGMENTS.

I am indebted for help and suggestions to Prof. Dr. J. E. W. Ihle, formerly Director of the Zoological Laboratory of the University of Amsterdam, where the material was sectioned ; to Dr. G. Barendrecht, Amsterdam, and Prof. Dr. J. de Wilde, Wageningen, the Netherlands ; and to Mr. S. G. Kiriakoff, Ghent, Belgium.

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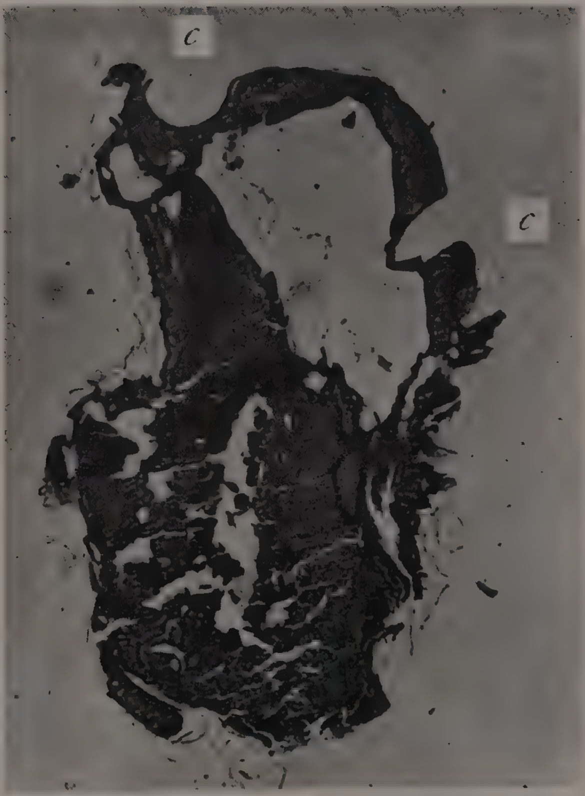
PLATE I.

Tremophora carycina Diakonoff, male. Antero-dorsal portion of the second abdominal segment; somewhat oblique transverse section. *c, c*—cavities of the dorsal organs.



Tremophora carycina Diakonoff, male.

A. Diakonoff.

Adlard & Son, Ltd., Dorking

BOYDAIA JORDANI SP. N., A NEW ENDOPARASITIC MITE (ACARINA : SPELEOGNATHIDAE).

By G. L. van Eyndhoven.
(*Zoologisch Museum, Amsterdam.*)

With 9 Text-figures.

The family Speleognathidae Womersley, 1936, was based on *Speleognathus australis* Womersley, 1936, a mite collected from moss in the field and perhaps not parasitic.

Since 1948, when Elizabeth Boyd described a second species, *S. sturni*, which was also the first species of this family found in the nasal cavities of birds, further nasal Speleognathidae have been discovered and it is most probable that others will follow.

In the year 1953 Womersley created the genus *Boydaia* for the species *Speleognathus sturni* Boyd, 1948, *S. striatus* Crossley, 1952, and his new mite, *B. angelae* Womersley, 1953, mainly based on palpal differences.

Recently, in 1954, Cooreman established another genus, *Speleognathopsis* for his new species *S. galli* Cooreman, 1954. This author, who considers the presence of eyes as being of more importance than differences in palpal characters, divides the family as follows: *Speleognathus australis* and *S. striatus* ; *Boydaia sturni* and *B. angelae* ; *Speleognathopsis galli.*

In my opinion it is not at all certain that *S. australis* normally lives in the noses of birds as is supposed by other authors. Various mucous substances exist in mosses and in the soil, *e.g.* by decomposition, and it is quite likely that Womersley's species feeds on such substrates.

The Zoologisch Museum at Amsterdam has received two specimens of *Turdus pilaris* L. (Fieldfare, Netherlands: Kramsvogel), found dead during migration, and from the nose of one I collected a fifth species of Speleognathidae, which is described below. I am pleased to name it *Boydaia jordani* sp. n., after my old friend and colleague in parasitology, in whose honour the present volume is published.

Some striking characters of the new species are: the broad-shouldered body, the plate-like structure of the greater part of the dorsal skin, the large basal rings of most of the hairs, fully developed palps, the relatively long legs (about as long as the body), and the absence of a hair on coxae IV.

I have placed the species in the genus *Boydaia*, although certain characters may justify a new genus later when more species have come to our knowledge.

Boydaia jordani sp. n.

Adult female.—One specimen. Idiosoma (mounted specimen): length 325 μ, breadth 260 μ. Gnathosoma and palps 90 μ.

Dorsum (fig. 1).—Dorsal skin more or less smooth, but a large plain area present, surrounded by a few wrinkles, which has the appearance of a dorsal plate with a vague outline, and which can be divided into a propodosomatic and an opisthosomatic area.

Dorsal setae all plumose, each originating from a large basal ring, except the four humeral setae, which have rings of normal size. These large rings resemble small shields ;

and are even more distinct ventrally. Setae of more or less even length, with the exception of the humeral setae, which are shorter. Sensory setae originate from a pore and are longer; close to them are the very minute setae verticales externae. Terminal dorsal hairs longer, appearing to form a group with the two pairs of setae which are situated, at least in my specimen, ventrally close to the posterior body margin.

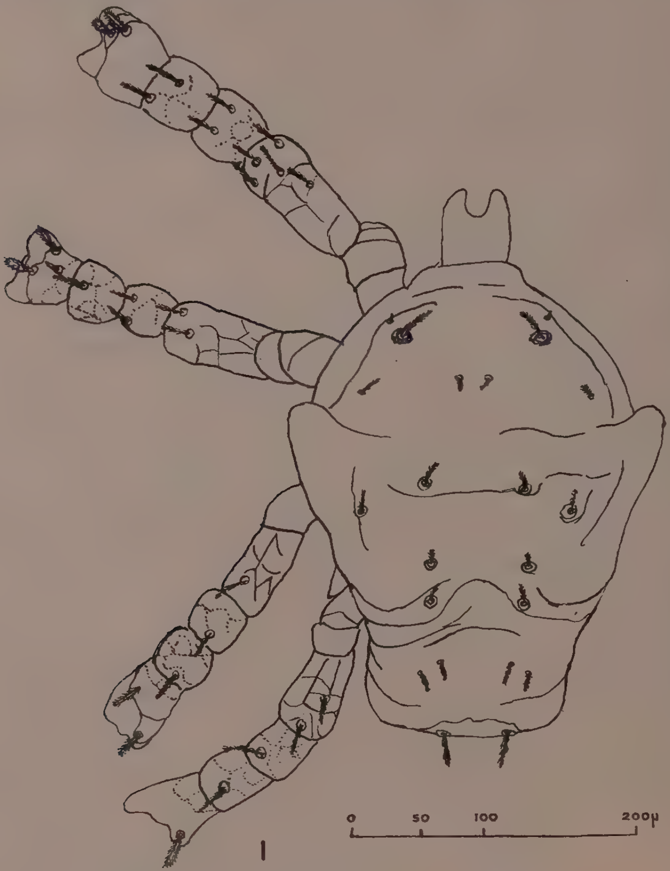


FIG. 1.—*Boydaia jordani* sp. n. ♀, Dorsal face.

General form of body broad-shouldered, truncated posteriorly.

Venter (fig. 2).—Ventral side smooth, with a distinct demarcation line between the two groups of coxae I and II and coxae III and IV. One pair of setae between coxae I, one between coxae III, and one between coxae IV.

Genital region formed by a round shield with a longitudinal split. Two pairs of setae near anterior margin of shield, and three setae on each half of shield itself. Posteriorly two pairs of longer setae present, as stated above, which form a group with the last pair of dorsal setae. All ventral hairs plumose and originating from large and very distinct basal rings, with the appearance of small shields.

Legs (figs. 1, 2).—Length, including coxae, as follows : I, 335 μ ; II, 315 μ ; III, 275 μ ; IV 315 μ.

Each coxa with a large smooth area, from which internally some small areas are separated. Coxal hairs are 2, 1, 1 and 0. It is noteworthy that not only such an important hair as that of coxa IV may or may not be present (in *Boydaia sturni* and *Speleognathus striatus* it is present), but also that the coxal hairs of *Speleognathopsis galli* are still more variable.

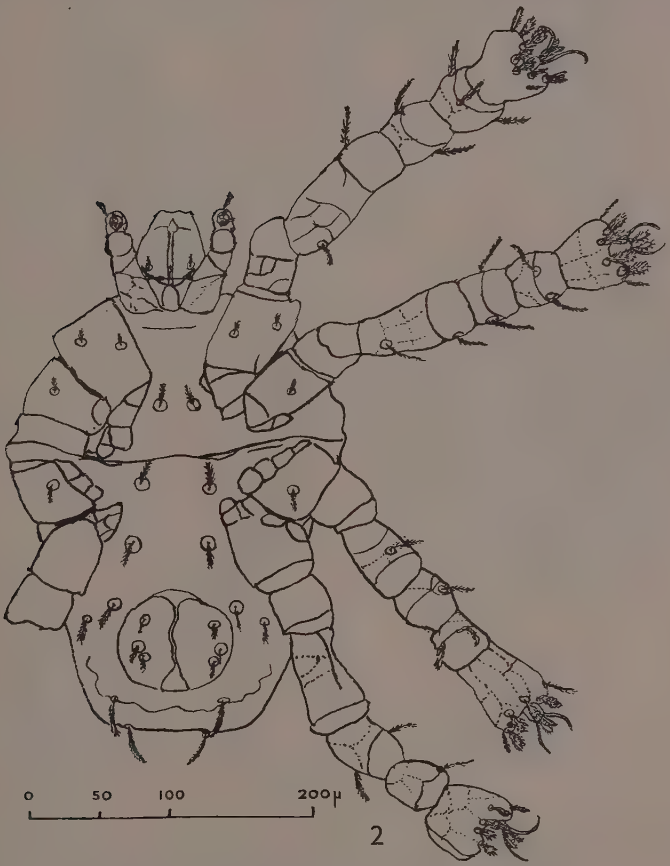


FIG. 2.—*Boydaia jordani* sp. n. ♀, Ventral face.

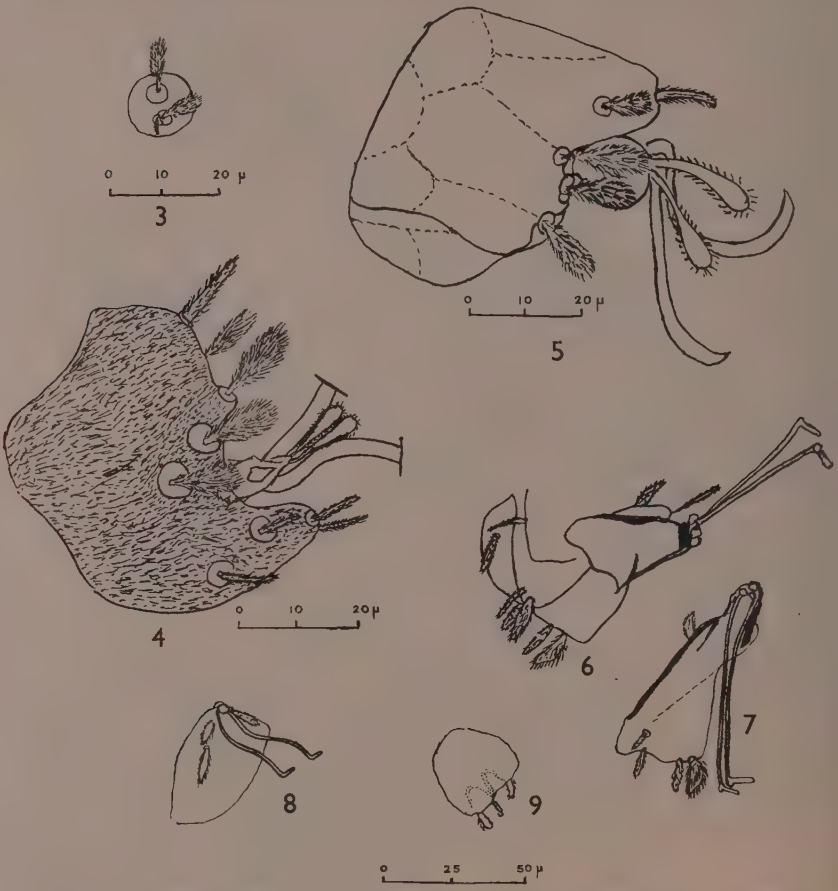
Legs relatively long, about as long as body, their setae as illustrated. Large basal rings present. Lateral hairs point a little downward, so that they have been indicated on the sketch of the ventral face. Various segments show the remarkable reticulation of Speleognathidae, either quite distinct (straight lines) or more vague (broken lines). Although the ventral side of tarsi II, III and IV is reticulated, this is not the case with tarsus I.

Legs stout, the tarsi broadened. Hairs on tarsi (figs. 4, 5) show different structures adapted to their respective functions.

Structure of skin of legs not easily described, being so very fine as to appear velutinous, but no real hairs present. In this skin the large basal rings of the setae show distinct and smooth areas.

Gnathosoma.—Its details not clear in my specimen.

Palpi.—Palpi completely developed, there appearing to be four free segments. Palpal tarsus attached ventrally and bears three plumose hairs, two of which are combined to form one group (fig. 3).



FIGS. 3–9.—*Boydaia jordani* sp.n. (3) Tarsus of left palp, ventrally. (4) Tarsus I, ventrally. (5) Tarsus IV, ventrally. (6)–(7) Larva, left and right tarsal joints of leg I. (8) Larva, tarsal joint of leg II. (9) Larva, tarsal joint of leg III.

Larva.—My only specimen is mutilated, so that no complete description can be given. For the sake of completeness, however, four sketches of leg fragments are given, as far as they are visible. I observe that Boyd has already mentioned prominent claws for the larva of *Boydaia sturni*. Crossley, for *Speleognathus striatus*, makes no special reference. As far as can be seen, my larva has two long, straight claws on tarsus I, two smaller and somewhat bent on tarsus II, whilst tarsus III bears two normal claws.

Holotype, 1 ♀. Type host *Turdus pilaris* L., in the nasal cavities. Migrating birds of Fennoscandinavian origin, found dead at Kampen, Netherlands, 24.ii.1954. In Zoologisch Museum, Amsterdam, slide loc. 954138.

Larval type.—Same details, slide loc. 954138.

The mites were in the central part of the nose, not as far back as is generally the case for *Boydaia sturni* from *Sturnus vulgaris*. The trachea has not been inspected. No specimens were found in the nose of the second bird. So far, mites of this family have not been seen by me from other *Turdus* species (*T. merula* L., *T. musicus* L., *T. ericetorum* Turt.) which I received for inspection.

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"In some of the species [of the Arctiid genera *Ammalo* and *Sychesia*] we find small but obvious morphological differences in the specimens from certain localities: geographical varieties or **subspecies.** In other forms which are also geographically separated the differences are so great that we must consider them specific; these species replace one another, one being a substitute for the other: **vicariant species**. And lastly, we have species the ranges of which overlap or are more or less the same, the species occurring side by side, often actually flying together: **synpatric species** . . . If the differences in the first category become greater, we have the second. If the range of the second category extends, we have the third category of forms. This is true not only for insects, but also for other classes of animals, the exceptions appearing to me more seeming than real. The important part which geographical isolation plays in the evolution of the subspecies and vicariant species is so obvious that it is hardly necessary to dilate on it."

(Jordan, K., 1916, *Novit. zool.* **23** : 150.)

SYNOPSIS DER AFRIKANISCHEN GATTUNGEN DER COCHLIDIIDAE (LEPIDOPTERA).

von Erich Martin Hering.

(*Zoologisches Museum der Humboldt-Universität zu Berlin.*)

Die in so zahlreichen Gattungen und Arten über den grössen Teil der Erde verbreitete Familie der Cochlidiidae (Limacodidae) hat im Zoologischen Museum Berlin seit langer Zeit immer eine besondere Aufmerksamkeit gefunden. Bereits mein Vorgänger F. Karsch hat diesen Lepidopteren stets eine besondere Liebe entgegengebracht, eine Neigung, die ich von ihm übernommen und jahrzehntelang weiter kultiviert habe. So ist im Verlaufe von mehr als einem halben Jahrhundert eine recht reichhaltige Sammlung von Angehörigen dieser Familie zusammengebracht worden, bereichert namentlich auch durch den Ankauf des Materials aus der Sammlung Oberthür. Das Berliner Museum war bis zum Weltkrieg I vorwiegend auf afrikanisches Material eingestellt gewesen, das deshalb besonders reichlich hier vertreten ist ; nach dieser Zeit erfolgte eine gleichmässige Berücksichtigung aller Regionen. Der Reichtum an afrikanischen Arten legt es nahe, die generische Zusammengehörigkeit und die phyletischen Zusammenhänge der Vertreter dieser Gruppe einmal eingehend zu untersuchen, wozu in der folgenden Zusammenstellung eine kleine Vorarbeit gegeben werden soll.

Vor fast 60 Jahren hatte F. Karsch (1896) eine erste Ordnung und Übersicht der Arten dieser Familie veröffentlicht, in der eine Anzahl neuer Gattungen von ihm aufgestellt wurden. Er schuf eine für die damalige Zeit gut brauchbare analytische Übersicht der Gattungen, in die er die Arten einordnete. Mehr als eine Erweiterung dieser Arbeit unter Berücksichtigung des heutigen Bestandes an Arten und Gattungen wird in meinem vorliegendem bescheidenen Beitrag noch nicht mitgeteilt werden. Die analytische Schlüsselung der Gattungen wird als Grundlage auch nur die äussere Morphologie verwenden, wird aber durch Hinzunahme bisher nicht verwendeter Besonderheiten im Körperbau eine vorläufige generische Einordnung der Arten ermöglichen.

Dass damit eine endgültige Fassung und Umgrenzung der Gattungen und ihre phyletische Zuordnung nicht erreicht werden kann, liegt auf der Hand. Eine moderne Gattungs-Systematik, die auch phyletischen Betrachtungen Genüge leistet, ist nur möglich, wenn die Charakterisierung der Gattungen nach der äusseren Morphologie erhärtet wird durch die Kennzeichnung der Kopulations-Apparate, namentlich der ♂. Deren Merkmale sind bei der generischen Kennzeichnung und Differenzierung einer Familie allen übrigen morphologischen Befunden überzuordnen. Eine Darstellung des Baues der Sexual-Armaturen der Cochlidiidae, die künftiger Bearbeitung zugewiesen wird, kann erst den Gattungswert der bisherigen Klassifizierung herausstellen und eine richtige Gattungsanordnung nach phyletischen Gesichtspunkten gewährleisten. Der vorliegende Beitrag kann also vorerst nur taxonomischen Bedürfnissen abhelfen.

Für deren Befriedigung ist die Heranziehung einiger weiterer Merkmale als bisher erfolgt, die in der Vergangenheit noch nicht berücksichtigt worden sind. Unter ihnen ist die Ausbildung der basalen Media innerhalb der Mittelzelle der Flügel besonders zu erwähnen. Ihr Erhaltungszustand kennzeichnet ja im Zusammenhang mit der der Analis in beiden Flügeln als ausgebildeter Adern die Hinzurechnung der Familie zu den " Microlepidoptera ". Besonderes Augenmerk wurde auf ihre Gabelung innerhalb der Mittelzelle (ursprünglicher Zustand) oder der Einschmelzung der Gabeläste zugewendet, wobei die Erhaltung der echten Querader als Abschluss der Gabel als besonders beachtenswert angesehen wurde. Ferner erschien vielfach wichtig, ob Vorder-oder Hinterecke der Mittelzelle in beiden Flügeln ein stärkeres, zipfelartiges Vorspringen gegen den Flügelsaum aufwiesen.

Umstritten ist vielfach die Frage, ob es zulässig ist, " sekundäre " (besser tertiäre) Geschlechtsmerkmale, wie etwa die Ausbildung der Fühler des ♂, zur generischen Kennzeichnung oder Differenzierung heranzuziehen. Der reine Taxonom verneint meistens diese Frage; denn er wird sich dann, einem einzelnen ♀ gegenübergestellt, vielfach ausser Stande sehen, eine Determination vornehmen zu können. Wenn man aber zur Gattungsbegründung die eigentlichen sekundären Geschlechtsmerkmale des ♂, die Kopulationsapparate, als in erster Linie massgeblich ansieht, soll man doch auch die tertiären Merkmale dabei beachten, wenn auch ihre Bedeutung der der sekundären unbedingt unterzuordnen ist, da sie vielfach als Konvergenzbildungen auftreten, wie etwa die Untersuchungen der letzten Zeit an Tortricidae besonders deutlich gezeigt haben. Dass man aber die Merkmale nur eines Geschlechtes überhaupt für die Klassifizierung heranzieht, ist durchaus kein Verbrechen und hat seine volle Berechtigung; denn ♂ and ♀ stellen eine biologische Einheit dar, und von einer solchen sprechen wir, wenn wir eine Art, Unterart etc. und damit auch die höheren Kategorien kennzeichnen. Unter diesem Gesichtspunkt sind im folgenden Beitrag auch die Fühler des ♂ mit verwendet worden, wenn auch, wo irgend möglich, Kennzeichen, die beiden Geschlechtern gemeinsam sind, vorwiegend oder wenigstens zusätzlich herangezogen worden sind.

Die (als Larve parasitisch lebenden) Epipyropidae, die anscheinend oder scheinbar den Cochlidiidae sehr nahe stehen, sind bei der folgenden Gattung-Schlüsselung ausser Betracht gelassen worden. Es scheint, als ob sie eine wohl gesonderte Familie darstellen, wofür namentlich die zu einem unpaarigen Kegel reduzierten Mundteile und die einfache oder vereinfachte Ausbildung des Uncus der Sexualarmatur des ♂ sprechen, der hier einem gewöhnlichen Tergit ähnelt.

Cochlidiidae, wie sie nachfolgend aufgefasst werden, sind Frenatae, bei denen die folgenden Kennzeichen gleichzeitig vorhanden sind: Rüssel und Maxillarpalpen rudimentär oder fehlend. Chaetosema und Tympanalorgan fehlend. Analis und Basalteil der Media (in der Mittelzelle) in beiden Flügeln wenigstens proximal als sklerotisierte Adern vorhanden. Areola in der Mittelzelle der Vorderflügel stets fehlend (bei Cossidae meist vorhanden). Die *sc* im Hinterflügel, wenn vorhandenmeist, durch Querader oder Anastomose mit dem Vorderrand der Mittelzelle verbunden. Frenulum vorhanden (bei den Chrysopolomidae fehlend). Nach B. Alberti (mündlich) unterscheiden sich die den Cochlidiidae am nächsten stehenden Zygaenidae dadurch, dass bei diesen niemals gleichzeitig Chaetosema und entwickelter Rüssel fehlen; wenn bei Zygaenidae der Rüssel reduziert ist, ist doch wenigstens ein Chaetosema vorhanden. Bei Cochlidiidae fehlen Chaetosema und entwickelter Rüssel immer.

Den afrikanischen Metarbelidae, die oft Cochlidiiden im Habitus ähnlich sind, fehlt die ausgebildete Analis in beiden Flügeln wie auch das Frenulum. Der Museologe erkennt Angehörige der Familie der Cochlidiidae auf den ersten Blick an einem eigentümlichem matten Seidenschimmer der Flügelunterseite, von dem sich die Flügeladern abheben, der sich jedoch nicht definieren lässt.

Es erfolgte auch die Einschlüsselung einiger Gattungen, die nur ausserhalb der afrikanischen Region vorkommen, um die Nichtzugehörigkeit afrikanischer Arten, die in solchen Gattungen beschrieben worden sind, so zu erweisen. Im übrigen umfasst dieser Beitrag die Gattungen, die im aethiopischen Raum + Madagascar vorkommen. Die Gattungen aus dem palärktischen Teile des Kontinentes (Nordafrika) blieben unberücksichtigt.

Nicht von allen Gattungen haben mir Vertreter vorgelegen. Genera, die ich nicht in natura untersuchen konnte und nur auf Grund der Beschreibung in die Tabelle aufgenommen worden sind, wurden mit einem * vor dem Gattungnamen gekennzeichnet. Ganz unberücksichtigt, weil auch nach der ungenügenden Beschreibung nicht einzuordnen, blieben folgende in Afrika vertretenen zu der Familie angeblich gehörenden Gattungen, die van Eecke (1925) im *Catalogus Lepidopterorum* Pars 32 anführt, oder die später beschrieben wurden:

**Gavara* Walker, 1857 (= *Heterolepis* Felder, 1874); **Inous* Walker, 1855; **Lembopteris* Butler, 1898; **Paragetor* Bethune-Baker, 1911; **Probalintha* Walker, 1865; **Pseudolimacodes* Viette, 1951. Es ist besonders erfreulich, dass Herr Harry K. Clench begonnen hat, die nach Beschreibung vielfach nicht deutbaren Arten von Holland durch Typenuntersuchung zu klären und zu deuten.

Adrallia Walker, 1865, ist Lymantriide; *Scirrhoma* Bethune-Baker, 1915 gehört p.p. zu *Hadraphe* Karsch und p.p. zu *Andrallochroma* Karsch. Zu *Latoia* Guerin, 1844, sind zu rechnen auch *Asteria* Felder, 1871, *Parasa* Moore, 1859 und *Somara* Walker, 1855. Weitere Synonym-Setzungen finden sich in meiner Bearbeitung der Familie in Seitz, 1928, *Grossschmetterlinge der Erde* **14**: 447–476.

BESTIMMUNGSTABELLE DER AFRIKANISCHEN COCHLIDIIDEN-GATTUNGEN.

1. Media der Hinterflügel innerhalb der Mittelzelle gegabelt. Im Vorderflügel mündet der hintere Mediaast innerhalb der Mittelzelle zwischen dem Ursprung von Ader cu_1 und m_2. Ader Rs(8) im Hinterflügel ganz frei, nicht durch Querader mit dem Zellvorderrand verbunden . . . . Subfam. **Crothaeminae.** 2

– Media der Hinterflügel in der Mittelzelle einfach. Im Vorderflügel mündet der hintere Mediaast in der Mittelzelle vorderrandwärts von m_2, oder Media dort einästig oder rückgebildet
Subfam. **Cochlidiinae.** 4

2. Im Vorderflügel Ader r_{3+4} gestielt. Retinaculum fehlend
Crothaema Butler, 1880
Typische Art: *C. sericea* Butler, 1880

– Im Vorderflügel alle Adern frei aus der Mittelzelle entspringend. Retinaculum beim ♂ vorhanden 3

3. Fühler in beiden Geschlechtern mit Kammzähnen
Caffricola Hampson, 1919
Typische Art: *C. cloeckneria* (Cramer, 1782)

– Fühler höchstens mit bewimperten Sägezähnen. **Arctozygaena** Gaede, 1926

Typische Art: *A. quinquemaculata* Gaede, 1926

4. Im Vorderflügel cu_1 und cu_2 gestielt 5

– Beide Adern getrennt entspringend 8

5. Im Vorderflügel r_{3+4} verschmolzen, daher eine Ader fehlend *__Paraplectra__ Bethune-Baker, 1912

Typische Art: *P. modesta* Bethune-Baker, 1912

– r_3 und r_4 nur gestielt, Geäder vollständig 6

6. Vorderflügel am Innenrand mit Schuppenzahn, t_3 mit nur 1 Spornpaar, r_1 und r_2 im Vorderflügel stark nach vorn konvex **Trachyptenidia** Hering, 1928

Typische Art: *T. incredibilis* Hering, 1928

– Vorderflügel am Innenrand ohne Schuppenzahn 7

7. Im Vorderflügel nur r_{3+4} gestielt, t_3 mit 2 Spornpaaren. Im Hinterflügel sc von der Mitte des Mittelzellen-Vorderrandes abgehend *__Featheria__ Hampson, 1916

Typische Art: *F. obvia* Hampson, 1916

– Im Vorderflügel $r_2 - r_5$ gestielt. t_3 mit 1 Spornpaar **Zarachella** Jordan, 1915

Typische Art: *Z. specularis* Jordan, 1915

8. Im Hinterflügel rr und m_1 getrennt entspringend, etwa parallel . . 9

– rr und m_1 entspringen aus einem Punkt oder gestielt, und divergieren 13

9. Im Vorderflügel nur r_{3+4} gestielt 10

– Im Vorderflügel r_{2-5} gestielt 11

10. Fühler des ♂ mit Kammzähnen . . . . . . **Taeda** Wallengren, 1863

Typische Art: *T. aetitis* Wallengren, 1863

— Fühler auch beim ♂ einfach . . . . . . **Cochlidium** Hübner, 1822

Typische Art: *C. limacodes* (Hufnagel, 1776)

11. Fühler des ♂ in der Basalhälfte mit 2 Reihen von Kammzähnen . . 12

— Fühler des ♂ nur gekerbt, mit Wimperpinseln **Phlebodicha** Karsch, 1896

Typische Art: *Ph. afflata* Karsch, 1896

12. Im Hinterflügel sc nur nahe der Flügelwurzel mit dem Vorderrand der Mittelzelle anastomosierend, Hinterecke der Mittelzelle stark saumwärts vorspringend. Im Vorderflügel die Entfernung $cu_2 - cu_1$ 2–3 mal so lang wie die $cu_1 - m_3$; r_1 basal stark nach vorn convex . . . . **Altha** Walker, 1862

Enthält nur orientalische Arten. Typische Art: *A. nivea* Walker, 1862

— Im Hinterflügel sc mit der Mitte des Vorderrandes der Mittelzelle durch Querader verbunden, gegen den Vorderrand überzählige Queräderchen entsendend. Hinterecke der Mittelzelle nur schwach vorspringend. Im Vorderflügel cu_2, cu_1 und m_3 in etwa gleichen Abständen, r_1 normal, höchstens schwach nach vorn convex **Alunus** Hering, 1935

Typische Art: *A. amatus* Hering, 1935

13. Vorderflügel am Innenrand mit einem Schuppenzahn, r_{2-4} gestielt. Fühler des ♂ nur gewimpert 14

— Vorderflügel am Innenrand ohne Schuppenzahn 15

14. Im Vorderflügel cu_2 bis m_3 sehr stark gekrümmt. Palpen vorgestreckt . . . . *__Narosana__ Bethune-Baker, 1915

Typische Art: *N. agbaja* Bethune-Baker, 1915

— Im Vorderflügel cu_2 bis m_3 gleichmässig gebogen oder gerade. Palpen aufwärts gebogen . . . . **Trachyptena** Bethune-Baker, 1911

Typische Art: *T. rufa* Bethune-Baker, 1911

15. Flügel dünn mit basalwärts gerichteten Haaren bekleidet. Im Vorderflügel r_3 und r_4 aus einem Punkt entspringend. Fühler des ♂ ohne Kammzähne . . . . ***Collenettea** Talbot, 1927

Typische Art: *C. semiaurantia* Talbot, 1927

— Flügel mit den normalen, breiten Schuppen bekleidet 16

16. Im Vorderflügel r_3 und r_4 ganz verschmolzen oder erst ganz kurz vor dem Aussenrand gegabelt, mit r_2 und r_5 zusammen lang gestielt 17

— Gabeläste von r_{3+4} lang, nie verschmolzen 19

17. r_{3+4} im Vorderflügel verschmolzen. Tibialsporne fehlen. Fühler des ♂ mit bis zum Ende allmählich verkürzten Kammzähnen **Pseudolatoia** Hering, 1954

Typische Art: *Ps. viettei* Hering, 1954

— Diese Merkmale nicht vereint vorhanden 18

18. Im Vorderflügel r_{3+4} verschmolzen. Fühler des ♂ mit Kammzähnen, t_3 mit 2 Spornpaaren . . . . **Prolatoia** Holland, 1893

Typische Art: *Pr. perileuce* Holland, 1893

Hierher wahrscheinlich als Synonym: *Charistia* Hering, 1928 (typische Art: *Ch. satanas* Hering, 1928).

— r_{3+4} verschmolzen oder erst kurz vor dem Saum gegabelt. Fühler des ♂ einfach . . . . **Pseudomantria** Bethune-Baker, 1911

Typische Art: *Ps. flava* Bethune-Baker, 1911

19. Im Hinterflügel rr und m_1 verschmolzen, daher eine Ader fehlend, sc bei der Mitte des Mittelzellen-Vorderrandes mit diesem durch Querader verbunden. Im Vorderflügel r_{2-5} gestielt, t_3 mit 1 Spornpaar . . . . **Erotomania** Hering, 1930

Typische Art: *E. schoutedeni* Hering, 1930

— Hinterflügel mit vollständigem Geäder, rr und m_1 gestielt oder aus einem Punkte entspringend 20

20. Alle Schenkel stark verdickt. Fühler des ♂ bis zur Mitte mit Kammzähnen. Im Vorderflügel r_{2-4} gestielt, r_5 von diesem Stiel entfernt entspringend . . . . ***Oidemaskelis** Bethune-Baker, 1915

Typische Art: *Oi. eurota* Bethune-Baker, 1915

— Beine normal ausgebildet 21

21. t_3 mit nur 1 Spornpaar oder auch dieses fehlend 22

— t_3 mit 2 Spornpaaren 43

Hintertibien höchstens mit 1 Paar von Spornen:

22. Fühler des ♂ nur gewimpert. Vorderflügel schwarzbraun, mit 3 gezähnten Silberlinien (Madagascar) . ***Thliptocnemis** Mabille, 1900

Typische Art: *Th. barbipes* Mabille, 1900

— Diese Merkmale nicht vereint vorhanden 23

23. Palpen lang schnauzenförmig vorgestreckt, ihr 3. Glied so lang oder länger als das 2. Im Hinterflügel sc nahe der Wurzel mit dem Vorderrand der Mittelzelle anastomosierend . . **Hyphorma** Walker, 1865

Typische Art: *H. minax* Walker, 1865

H. subterminalis Hampson, 1910, von der Goldküste beschrieben, gehört vielleicht anderer Gattung an.

— Palpen nicht so lang, ihr 3. Glied kürzer 24

24. Palpen kurz, ihr Endglied höchstens 1/3 so lang wie das vorletzte, oft unter dessen Behaarung verborgen. Sind sie länger dann fehlen aber doch Silberzeichnungen an den Beinen 25

— Palpen verlängert, vorstehend, ihr Endglied etwa 1/2 so lang wie das vorletzte. Vorderbeine silberweiss gefleckt . **Ctenocompa** Karsch, 1896

Typische Art: *Ct. hilda* (Druce, 1887)

25. Dorsale Bekleidung der Tarsen am Ende verbreitert, schuppenförmig. Im Vorderflügel r_1 mit r_{2-5} gestielt (wenn r_1 isoliert und m_2 an m_3 genähert, cf. *Trogocrada*. Punkt 27!) 26

— Tarsenbekleidung zugespitzt, haarförmig 28

26. Hinterecke der Mittelzelle des Vorderflügels nicht vorgezogen. Fühler-Kammzähne des ♂ zur Spitze hin allmählich verkürzt. Im Vorderflügel entspringt m_2 in der Mitte zwischen m_1 und m_3 . . . 27

— Hinterecke der Mittelzelle im Vorderflügel stark saumwärts vorspringend, m_2 an m_3 genähert. Fühler des ♂ in der Endhälfte ohne Kammzähne . . . . **Euclea** Hübner, 1822

Typische Art: *E. cippus* (Cramer, 1775)

Amerikanische Gattung. Die von Ogove beschriebene *E. brunnea* Holland, 1893, gehört sicherlich in eine andere Gattung.

27. Im Vorderflügel die Mediagabel distal durch eine Querader abgeschlossen, m_2 in der Mitte zwischen m_1 und m_3, r_2 mit r_{3-5} gestielt. Im Hinterflügel die Hinterecke der Mittelzelle stark saumwärts vorgezogen . . . . **Sporetolepis** Karsch, 1899

Typische Art: *Sp. subpellucens* Karsch, 1899

— Mediagabel distal offen, m_2 an m_3 genähert, r_1 entspringt frei aus der Mittelzelle. Im Hinterflügel hintere Ecke der Mittelzelle nicht vorgezogen . . . . **Trogocrada** Tams, 1953

Typische Art: *T. deleter* Tams, 1953

28. Im Hinterflügel sc an der Mitte des Vorderrandes der Mittelzelle mit ihm anastomosierend oder durch Querader verbunden, oder noch weiter saumwärts. Fühler des ♂ nur in der Basalhälfte mit 2 Reihen von Kammzähnen 29

— Anastomose oder Querader des Hinterflügels näher der Flügelwurzel 30

29. Mittelzelle des Vorderflügels sehr kurz, nur von halber Flügellänge. Vorderast der m in der Mittelzelle nur eine Falte. Im Hinterflügel sc stark nach vorn convex, Aussenrand concav . **Eccopa** Karsch, 1899

Typische Art: *E. oculita* Karsch, 1899

— Im Vorderflügel die Mittelzelle länger als 1/2 des Flügels. Beide Äste der basalen m in der Mittelzelle gleichstark . **Casphalia** Walker, 1866

Typische Art: *C. flavicollis* Walker, 1866

30. Im Vorderflügel entspringt r_1 viel weiter saumwärts als cu_2. Fühler des ♂ nur in der Basalhälfte mit Kammzähnen 31

— r_1 im Vorderflügel entspringt gegenüber cu_2 oder noch weiter wurzelwärts 35

31. Im Vorderflügel sind die beiden Gabeläste der m in der Mittelzelle nach aussen durch eine Querader abgeschlossen 32

— Die Mediagabel der Vorderflügel nach aussen offen, abschliessende Querader fehlt. Vorderflügel grün gezeichnet **Coenobasis** Felder, 1874

Typische Art: *C. amoena* Felder, 1874

32. Tibialsporne fehlen ganz . . . . **Latoiola** gen. n.

Typische Art: *L. albipuncta* (Holland, 1893)

— Sporne an t_3 vorhanden, wenn auch manchmal sehr klein 33

33. Im Vorderflügel die m in der Mittelzelle von ihrer Mitte an gegabelt. Palpen etwas abstehend behaart . . . . . **Delorrhachis** Karsch, 1896

Typische Art: *D. viridiplaga* Karsch, 1896

— Media in der Mittelzelle des Vorderflügels bei 1/3 ihrer Länge gegabelt, Palpen mehr angedrückt beschuppt 34

34. Fühler des ♂ bis zur Mitte doppelt kammzähnig. Hinterleib beim gespannten Falter die Hinterflügel nicht oder wenig überragend. Hinterecke der Mittelzelle im Hinterflügel stark saumwärts vorspringend . . . . **Miresa** Walker, 1855
Typische Art: *M.* (*guttifera* Walker, 1855 =) *albipuncta* (Herrich-Schäffer, 1854)

— Fühler des ♂ bis höchstens 1/3 mit Kammzähnen. Hinterleib die Hinterflügel weit überragend. Hinterecke der Mittelzelle im Hinterflügel wenig saumwärts vorgezogen, etwa bis gegenüber der Gabelung von rr und m_1 . . . . **Stroter** Karsch, 1899
Typische Art: *St. capillatus* Karsch, 1899

35. Im Vorderflügel die Media in der Mittelzelle nicht gegabelt, r_2 entspringt basal von r_5 aus dem Stiel r_{3+4} oder aus einem Punkt mit ihm. Fühler des ♂ bis 2/3 mit Kammzähnen . **Zinara** Walker, 1869
Typische Art: *Z. nervosa* Walker, 1869

— Im Vorderflügel Media in der Mittelzelle gegabelt, wenn auch zuweilen ihr Vorderast schwächer oder nur als Falte ausgebildet 36

36. Im Vorderflügel r_2 erst saumwärts von r_5 aus dem Stiel r_{3+4} entspringend. Vorderast der Media in der Mittelzelle nur als Falte ausgebildet. Fühler des ♂ bis zum Ende mit kürzer werdenden Kammzähnen . . . . **Omocena** Karsch, 1896
Typische Art: *O. syrtis* (Schaus and Clemens, 1893)

— r_2 entspringt proximal von r_5 aus dem Stiel r_{3+4} oder ungestielt aus der Mittelzelle 37

37. Im Vorderflügel die Querader zwischen m_1 und m_2 gerade, nicht gewinkelt. Fühler des ♂ bis zur Mitte kammzähnig 38

— Querader im Vorderflügel zwischen m_1 und m_2 1–2mal gewinkelt . 39

38. Palpen abstehend behaart. Grundfarbe der Vorderflügel weiss **Parapluda** Aurivillius, 1899
Typische Art: *P. invitabilis* (Wallengren, 1860)

— Palpen anliegend beschuppt. Vorderflügel dunkel **Phorma** Karsch, 1896
Typische Art: *Ph. pepon* Karsch, 1896

39. Im Vorderflügel Querader zwischen m_1 und m_2 nur 1mal gewinkelt 40

— Querader zwischen m_1 und m_2 2mal gewinkelt. Fühler des ♂ im basalen Drittel mit Kammzähnen. Vorderflügel oft mit grüner Zeichnung **Latoia** Guerin, 1844
Typische Art: *L. albifrons* Guerin, 1844

Hierzu ist als Synonym zu stellen: *Parasa* Moore, 1859 (typische Art *P. lepida* (Cramer, 1779).

40. Tibialsporne fehlen (höchstens ist ein winziger Rest der Endsporne an t_3 erkennbar) . . . . **Lemuria** gen. n.
Typische Art: *L. gracilis* (Butler, 1882)

— Tibialsporne vorhanden 41

41. Beim ♂ die Fühlerkammzähne plattenartig verwachsen, daher Fühler nur mit 1 Reihe von Kammzähnen. Im Vorderflügel r_5 mit r_{3+4} lang gestielt . . . . **Barilla** Dyar, 1899
Typische Art: *B. lineata* (Holland, 1893)

— Fühler des ♂ mit 2 Reihen von Kammzähnen (bei *Hilipoda*, cf. 42, das ♂ unbekannt, r_5 vom Stiel r_{3+4} getrennt) 42

42. Hinterecke der Vorderflügel-Mittelzelle saumwärts vorgezogen. m_2 entspringt mehr saumwärts als der Stiel von r_{3-5} aus der Mittelzelle. Im Hinterflügel die Hinterecke der Mittelzelle saumwärts vorspringend, rr und m_1 gestielt. Fühler des ♂ mit allmählich verkürzten Kammzähnen bis ans Ende . . . . **Chrysamma** Karsch, 1896

Typische Art: *Ch. purpuripulcra* Karsch, 1896

— Im Vorderflügel Hinterecke der Mittelzelle nicht, die Vorderecke aber stark saumwärts vorspringend. m_2 entspringt in gleicher Höhe mit dem Stiel r_{3+4} oder wurzelwärts davon. Im Hinterflügel die Hinterecke der Mittelzelle nicht vorspringend, rr und m_1 entspringen aus einem Punkte . . . . **Hilipoda** Karsch, 1896

Typische Art: *H. gravidipes* Karsch, 1896

Hintertibien mit 2 Spornpaaren:

43. (21) Im Vorderflügel die Media-Gabelung in der Mittelzelle nach aussen nicht durch Querader abgeschlossen, die Gabeläste etwa im rechten Winkel gestellt. Media deshalb scheinbar ungegabelt (oder auch rückgebildet) 44

— Mediagabelung durch Querader aussen abgeschlossen, die selten nur faltenartig ist; die Gabeläste trennen sich in spitzem Winkel, der vordere zuweilen nur faltenartig 73

Unberücksichtigt blieben hier die in eine der beiden Kategorien gehörenden **Lembopteris* Butler, 1898, **Inous* Walker, 1864 und **Probalintha* Walker, 1865.

44. Im Vorderflügel r_3 und r_4 getrennt entspringend, r_{2+3} gestielt, r_1 stark nach vorn convex, aus einem Punkt oder gestielt mit r_{2+3}. Media in der Mittelzelle rückgebildet. Im Hinterflügel sc vor der Mitte des Mittelzellen-Vorderrandes mit diesem anastomosierend **Pachyphlebina** Hering, 1928

Typische Art: *P. degenerata* Hering, 1928

— Im Vorderflügel r_{3+4} gestielt 45

45. Im Vorderflügel r_1 gleich nach dem Ursprung stark convex, an sc herangedrückt 46

— r_1 gerade oder nach vorn concav, höchstens jenseits ihrer Mitte an sc herangedrückt 49

46. Im Vorderflügel r_2 saumwärts von r_5 aus dem Stiel von r_{3+4} entspringend. In beiden Flugeln die Hinterecke der Mittelzelle stark saumwärts vorgezogen. Fühler des ♂ bis 2/3 mit 2 Reihen von Kammzähnen . . . . **Birthama** Walker, 1862

Typische Art: *B. obliqua* Walker, 1862

Orientalische Gattung, zu ihr gestellte afrikanische Arten gehören zu *Afrobirthama* gen. n. (cf. Punkt 71).

— Im Vorderflügel entspringt r_2 proximal von r_5 aus dem Stiel r_{3+4}. Hinterecke der Mittelzelle nicht in beiden Flügeln gleichzeitig saumwärts stark vorgezogen 47

47. Palpen kurz und dick, sie erreichen, angedrückt, nicht die Höhe des oberen Augenrandes. Fühler des ♂ mit zu Platten verschmolzenen, daher einreihig gestellten Kammzähnen . . . **Afraltha** gen. n.

Typische Art: *A. chionostola* Hampson, 1910

Bei der orientalischen Gattung *Altha* Walker, 1862, sind im Hinterflügel rr und m_1 getrennt, Fühler des ♂ mit 2 Reihen von Kammzähnen.

— Palpen länger und dünner, sie erreichen, angedrückt, die Höhe des oberen Augenrandes. Fühler des ♂ einfach, ohne Kammzähne . 48

48. Im Vorderflügel entspringt meistens r_1 mehr wurzelwärts als cu_2 aus der Mittelzelle, cu_1, m_3 und m_2 in gleichem Abstande, höchstens ist die Entfernung $cu_1 - m_3$ doppelt so lang wie die $m_3 - m_2$. Hinterecke der Mittelzelle im Vorderflügel nicht saumwärts vorspringend. Grundfarbe der Vorderflügel ockerfarben . . . . **Afronarosa** gen. n.

Typische Art: *A. africana* (Hering, 1932)

Im Habitus ähnliche orientalische *Narosa* Walker, 1855, haben im Vorderflügel m_3 und m_2 stark genähert, aber stark vorspringende Hinterecke der Mittelzelle.

— Im Vorderflügel r_1 und cu_2 etwa gegenüber entspringend oder r_1 entspringt weiter saumwärts, m_2 und m_3 stark genähert. Grundfarbe der Vorderflügel weisslich oder grau . . **Niphadolepis** Karsch, 1896

Typische Art: *N. nivata* Karsch, 1896

N. alianta Karsch, 1899, gehört zu *Afronarosa* gen. n. (Punkt 48), *N. lactea* Pagenstecher, 1903, und *sinistra* Hering, 1928, zu *Jordaniana* gen. n. (Punkt 68).

49. Im Vorderflügel entspringt r_2 saumwärts von r_5 aus dem Stiel r_{3+4}. Fühler des ♂ nur im Basaldrittel mit 2 Reihen von Kammzähnen **Thoseidea** gen. n.

Typische Art: *Th. lineapunctata* Bethune-Baker, 1911

— r_2 entspringt wurzelwärts von r_5 vom Stiel r_{3+4} oder frei aus der Mittelzelle 50

50. Im Hinterflügel sc um die Mitte oder saumwärts von der Mitte des Vorderrandes der Mittelzelle mit ihm anastomosierend oder durch Querader verbunden 51

— Anastomose oder Querader bei 1/3 des Mittelzellen-Vorderrandes oder noch weiter wurzelwärts 61

51. Palpen-Endglied länger als das Mittelglied. Fühler des ♂ einfach, ohne Kammzähne . . . . **Hadraphe** Karsch, 1899

Typische Art: *H. aprica* Karsch, 1899

— Palpen-Endglied kürzer als das Mittelglied 52

52. Im Vorderflügel entspringt r_5 getrennt vom Stiel r_{3+4} aus der Mittelzelle 53

— Im Vorderflügel r_5 aus einem Punkt oder gestielt mit dem Stiel r_{3+4} entspringend. Fühler des ♂ bis fast ans Ende mit 2 Reihen von Kammzähnen 54

53. Fühlerkammzähne beim ♂ plattenartig verwachsen, Fühler daher nur 1 reihig gekämmt (*Anilina*) 72

— Fühler des ♂ basal mit 2 Reihen von Kammzähnen **Paryphanta** Karsch, 1896

Typische Art: *P. fimbriata* Karsch, 1896

54. Im Vorderflügel entspringt r_1 wurzelwärts von cu_2. Im Hinterflügel mündet die Querader fast senkrecht in den Vorderrand der Mittelzelle (am Ursprung von $rr + m_1$) 55

— Im Vorderflügel entspringt r_1 gegenüber cu_2 oder noch mehr saumwärts. Im Hinterflügel mündet die Querader meist spitzwinklig in den Vorderrand der Mittelzelle 58

55. Palpen aufsteigend, angedrückt die Höhe des oberen Augenrandes erreichend oder überragend. Fühler des ♂ einfach, oder bis zum Ende, allmählich verkürzt, mit 2 Reihen von Kammzähnen 56

— Palpen schräg vorgestreckt, angedrückt den oberen Augenrand nicht erreichend. Abdomen ohne Rückenschöpfe . . **Brachia** Karsch, 1896

Typische Art: *B. argyrogramma* Karsch, 1896

56. Fühler des ♂ einfach. Querader im Vorderflügel mit ungleich langen Winkel-Schenkeln (*Monema*) 67

— Fühler des ♂ mit Kammzähnen. Die Schenkel des von der Querader im Vorderflügel gebildeten Winkels etwa gleichlang 57

57. Palpen-Endglied etwa 1/3 so lang wie das vorletzte. Fühlerwurzel ohne auffallenden Schuppenfleck. Abdomen mit starken basalen Rückenschöpfen . . . . **Scotinochroa** Butler, 1896

Typische Art: *Sc. inconsequens* Butler, 1896

Hierzu als Synonym: *Parathosea* Aurivillius, 1921 (typische Art: *P. peringueyi* Aurivillius, 1921).

— Palpen-Endglied wenigstens halb so lang wie das vorletzte. An der Fühler-Wurzel ein auffälliger, weisser Schuppenfleck (fehlt ein solcher, dann cf. *Monema*, Punkt 67!) . . **Semyrilla** Aurivillius, 1899

Typische Art: *S. lineata* (Holland, 1893)

58. Palpen-Endglied vom vorletzten kaum abgesetzt, kürzer als 1/4 des zweiten. Beim ♂ etwa die letzten 5 Fühlerglieder ohne Kammzähne. Im Hinterflügel die Vorderecke der Mittelzelle stark vorspringend, ihr Ende mit dem Ursprung von m_2 auf gleicher Höhe **Susicina** gen. n.

Typische Art: *S. pyrocausta* (Hampson, 1910)

— Palpen-Endglied deutlich abgesetzt, wenigstens 1/4 des vorletzten lang. Beim ♂ höchstens letztes Fühlerglied ohne Kammzähne. Im Hinterflügel Vorderecke der Mittelzelle weniger oder nicht saumwärts vorspringend, Ursprung von m_2 stets saumwärts davon . . 59

59. Im Hinterflügel sc an oder vor der Mitte des Vorderrandes der Mittelzelle mit ihm anastomosierend 60

— sc im Hinterflügel saumwärts von der Mitte des Vorderrandes der Mittelzelle mit ihm durch schräge Querader verbunden **Brachiopsis** Hering, 1933

Typische Art: *B. conjunctoides* Hering, 1933

60. Querader im Hinterflügel etwa senkrecht auf dem Vorderrand der Mittelzelle stehend. Fühler mit Kammzähnen von etwa 3 fachem Schaft-Durchmesser. Beschuppung des 2. Palpengliedes lateral zusammengedrückt . . . . . . **Prosternidia** Saalmüller, 1884

Typische Art: *Pr. metallica* Saalmüller, 1884

— Querader des Hinterflügels spitzwinklig auf dem Vorderrand der Mittelzelle stehend. Kammzähne der Fühler des ♂ wenigstens 5mal so lang wie die Dicke des Fühler-Schaftes. Das beschuppte 2. Palpenglied erscheint walzigrund . . **Lepidorytes** Aurivillius, 1899

Typische Art: *L. sulcata* Aurivillius, 1899

61. (50). Im Vorderflügel entspringt r_5 weit vom Stiel r_{3+4} getrennt. Fühler des ♂ bis zum Ende mit Kammzähnen 62

— Im Vorderflügel r_5 mit dem Stiel von r_{3+4} aus einem Punkte oder gestielt entspringend 63

62. Palpen länger als der doppelte Augendurchmesser. Beine lang, dünn, anliegend glattschuppig. Im Vorderflügel entspringt r_1 weit wurzelwärts von cu_2 . . . . **Afroplax** Hering, 1941

Typische Art: *A. didyma* Hering, 1941

— Palpen kürzer als der doppelte Augendurchmesser. Beine kürzer, abstehend haarschuppig. Im Vorderflügel entspringt r_1 etwa gegenüber cu_2 . . . . **Natada** Walker, 1855

Typische Art: *N. rufescens* Walker, 1855

Bei späterer Aufteilung der heterogen zusammengesetzen Gattung wird man auch die afrikanischen, hier beschriebenen Arten zu einer eigenen Gattung absondern müssen.

63. Im Hinterflügel die Hinterecke der Mittelzelle nicht oder kaum merklich saumwärts vorspringend. Palpen-Endglied winzig klein. Fühler des ♂ bis zur Spitze mit allmählich verkürzten Kammzähnen 64

— Im Hinterflügel die Hinterecke der Mittelzelle weit über die Vorderecke saumwärts vorspringend 66

64. Im Vorderflügel entspringt r_5 aus einem Punkt mit dem Stiel r_{4+5}. Hinterecke der Mittelzelle nicht so weit saumwärts reichend wie die Vorderecke . . . . **Stroteroides** Strand, 1912

Typische Art: *St. nigrisignata* Strand, 1912

— Im Vorderflügel r_5 mit r_{3+4} lang gestielt. Hinterecke der Mittelzelle so weit oder etwas weiter saumwärts reichend als die Vorderecke 65

65. Im Hinterflügel rr und m_1 lang gestielt, sc mit dem Vorderrand der Mittelzelle kurz anastomosierend . . . . **Micraphe** Karsch, 1896

Typische Art: *M. lateritia* Karsch, 1896

— Im Hinterflügel entspringen rr und m_1 aus einem Punkt, sc mit dem Vorderrand der Mittelzelle durch schräge Querader verbunden ***Rhypteira** Holland, 1893

Typische Art: *Rh. sordida* Holland, 1893

66. Palpen-Endglied gut abgesetzt, wenigstens 1/3 so lang wie das 2. . 67

— Palpen-Endglied winzig klein, nicht abgesetzt, oft unter der Behaarung verborgen, weniger als 1/4 des vorletzten lang 69

67. Palpen-Endglied wenigstens halb so lang wie das vorletzte, seine Spitze den Scheitel überragend. Fühler des ♂ einfach **Monema** Walker, 1855

Typische Art: *M. flavescens* Walker, 1855

— Palpen-Endglied kürzer als die Hälfte des vorletzten, den Scheitel nicht überragend 68

68. Im Hinterflügel die Anastomose zwischen sc und dem Vorderrand der Mittelzelle nahe der Basis des Flügels. Fühler des ♂ mit 2 Reihen von Kammzähnen . . . . **Tetraphleba** Strand, 1921

Typische Art: *T. brevilinea* (Walker, 1855)

Orientalische Gattung. Ob *T. ruficeps* (Hampson, 1909) hierher gehört, ist noch zu untersuchen.

— Anastomose von sc mit der Mittelzelle des Hinterflügels an oder jenseits der Mitte des Mittelzellen-Vorderrandes. . . **Jordaniana** gen. n.

Typische Art: *J. lactea* (Pagenstecher, 1903)

69. Im Vorderflügel entspringt r_1 wurzelwärts von cu_2 aus der Mittelzelle 70

— r_1 im Vorderflügel entspringt gegenüber oder saumwärts von cu_2 . 71

70. Mittelsporne von t_3 etwa an der Schienenmitte! Fühler des ♂ mit 2 Reihen von Kammzähnen . . . . **Macroplectra** Hampson, 1892

Typische Art: *M. minutissima* (Swinhoe, 1890)

— Mittelsporne der t_3 weit distal von der Schienenmitte. Beim ♂ die Kammzähne der Fühler plattenartig verwachsen, Fühler daher nur einreihig gekämmt . . . . **Gephyrophora** Karsch, 1896

Typische Art: *G. mitis* Karsch, 1896

71. Im Vorderflügel entspringt r_2 vom Stiel r_{3+4} getrennt. Fühler des ♂ nur in der Basalhälfte mit 2 Reihen von Kammzähnen **Afrobirthama** gen. n.

Typische Art: *A. flaccidia* (Druce, 1899)

— Im Vorderflügel r_2 meist aus einem Punkt oder gestielt mit r_{3+4}. Fühler des ♂ bis zum Ende, allmählich verkürzt, mit Kammzähnen 72

72. Fühler des ♂ mit plattenartig verwachsenen Kammzähnen, daher nur einreihig kammzähnig. Im Vorderflügel r_5 aus einem Punkte oder getrennt von r_{3+4} . . . . **Anilina** Hering, 1937

Typische Art: *A.* (*plebeia* (Karsch, 1899) =) *divisa* (Holland, 1893)

— Fühler des ♂ mit 2 Reihen von Kammzähnen. Im Vorderflügel r_5 immer mit r_{3+4} gestielt . . . . **Thosea** Walker, 1855

Typische Art: *Th. unifascia* Walker, 1855

Orientalische Gattung. *Th. lineapunctata* Bethune-Baker gehört zu *Thoseidea* gen. n., cf. Punkt 49.

Im Vorderflügel Mediagabel nach aussen durch Querader abgeschlossen.

73. (43) Im Hinterflügel sc an oder jenseits der Mitte des Mittelzellen-Vorderrandes durch lange, schräge Querader mit ihm verbunden 74

— sc im Hinterflügel vor der Mitte des Mittelzellen-Vorderrandes mit ihm durch Anastomose oder Querader verbunden 76

74. Im Hinterflügel sc mit dem Vorderrand der Mittelzelle kurz vor dessen Ende verbunden. Im Vorderflügel r_1 gegenüber cu_2 entspringend. Fühler des ♂ bis etwa 2/3 mit 2 Reihen von Kammzähnen . . . . **Xanthopteryx** gen. n.

Typische Art: *X. confusa* (Walker, 1865)

— sc im Hinterflügel mit dem Mittelzellen-Vorderrand etwa an dessen Mitte verbunden. r_1 im Vorderflügel oft proximal von cu_2 entspringend 75

75. Beide Äste der Mediagabel in der Mittelzelle des Vorderflügels gleichstark. t_3 dünn behaart. Fühler des ♂ mit plattenartig verschmolzenen Kammzähnen, daher (bis 2/3) nur 1 reihig kammzähnig (*Gephyrophora*) 70

— Vorderer Media-Ast deutlich schwächer als der hintere. Hinterecke der Mittelzelle im Vorderflügel nicht oder kaum vorspringend. t_3 dick behaart. Fühler des ♂ bis zum Ende mit 2 Reihen von allmählich kürzer werdenden Kammzähnen besetzt. Vorderflügel mit einem weissen Mittelfleck . . . . **Cosuma** Walker, 1855

Typische Art: *C. rugosa* Walker, 1855

Wenn die langen Kammzähne der Fühler des ♂ bei 3/4, plötzlich abgesetzt, in Sägezähne übergehen, die Hinterecke der Mittelzelle der Vorderflügel saumwärts weit vorspringt und ein weisser Mittelfleck auf ihnen fehlt, dann cf. *Susica* Walker, Punkt 83!

76. Beim ♂ Saum der Hinterflügel concav. Fühler zu 1/3 kammzähnig. Beim ♀ Palpen-Endglied 1/3 des 2. lang, schwarz **Andrallochroma** Karsch, 1899

Typische Art: *A. melampepla* (Holland, 1893)

— Saum des Hinterflügels convex, Palpen-Endglied kürzer als 1/3 des vorletzten 77

77. Im Hinterflügel sc mit dem Vorderrand der Mittelzelle durch lange, schräge Querader verbunden (die zuweilen fehlen kann), oder es ist nur ganz nahe der Wurzel eine Anastomose vorhanden 78

— sc mit dem Vorderrand der Mittelzelle im Hinterflügel durch eine nicht ganz nahe der Flügelwurzel liegende Anastomose oder ein kurzes, etwa senkrecht stehendes Aderstück verbunden . . . 80

78. Im Vorderflügel die Hinterecke der Mittelzelle stark saumwärts vorspringend, r_1 entspringt viel weiter basal als cu_2. Fühler des ♂ bis zur Mitte mit Kammzähnen . . . . **Tryphax** Karsch, 1896

Typische Art: *T. vigoratus* Karsch, 1896

— Hinterecke der Mittelzelle im Vorderflügel kaum vorspringend. Fühler des ♂ bis zum Ende mit allmählich verkürzten Kammzähnen, oder einfach, ohne Kammzähne überhaupt 79

79. In der Mittelzelle des Vorderflügels der vordere Gabelast der Media schwächer als der hintere. Fühler des ♂ mit 2 Reihen von Kammzähnen. Vorderflügel mit hellem Mittelfleck (*Cosuma*) 75

— Beide Gabeläste der Media im Vorderflügel gleichstark. Fühler stets einfach, ohne Kammzähne . . . . . **Macrosemyra** Butler, 1882

Typische Art: *M. tenebrosa* Butler, 1882

80. Fühler des ♂ mit plattenartig verschmolzenen Kammzähnen, daher einreihig kammzähnig. Vorderbeine oder ein Basalschopf der Fühler silberweiss gefleckt 81

— Vorderbeine und Fühlerbasis ohne Silberzeichnung 82

81. Im Vorderflügel die Querader zwischen m_2 und m_3 gewinkelt. Vorderast der Media in der Mittelzelle schwächer als der hintere; der stärkere Hinterast mündet vorderrandwärts vom Ursprung von m_2. Palpen des ♀ verlängert, ihr Endglied mehr als halb so lang wie das Mittelglied . . . . **Teinorrhyncha** Holland, 1893

Typische Art: *T. umbra* Holland, 1893

Wie Herr Harry K. Clench feststellte, ist zu dieser Gattung und Art *Ctenolita* Karsch, 1896, typische Art *Ct. epargyra* Karsch, 1896, synonym.

— Im Vorderflügel Querader zwischen m_2 und m_3 gerade. Media-Äste in der Mittelzelle gleichstark, der hintere mündet innenrandwärts von m_2. Palpen des ♀ nicht verlängert . . . . **Apluda** Wallengren, 1863

Typische Art: *A. plebeia* Wallengren, 1863

82. Im Vorderflügel die Gabeläste der Media in der Mittelzelle kurz: Media erst saumwärts vom Ursprung des cu_2 gegabelt. Fühler des ♂ in der Basalhälfte mit 2 Reihen von Kammzähnen (*Afrobirthama*) 71

— Im Vorderflügel Gabeläste der Media in der Mittelzelle lang: Gabelung am Ursprung von cu_2 oder noch wurzelwärts davon 83

83. Fühler des ♂ bis zum Ende mit allmählich verkürzten Kammzähnen 84

— Fühler des ♂ bis 3/4 mit langen Kammzähnen das abgesetzte Endviertel nur mit kurzen Sägezähnen . . . . **Susica** Walker, 1855

Typische Art: *S. pallida* Walker, 1855

Orientalische Gattung. *S. pyrocausta* Hampson, 1910, gehört zu *Susicina* g.n., cf. Punkt 58, *S. confusa* Walker, 1865, zu *Xanthopteryx* g.n., cf. Punkt 74.

84. Beide Media-Äste in der Mittelzelle des Vorderflügels gleichstark. Fühler des ♂ mit 2 Reihen von Kammzähnen . . **Hegetor** Karsch, 1899

Typische Art: *H. herculeus* Karsch, 1899

— Vorderast der basalen Media im Vorderflügel schwächer. Beim ♂ Kammzähne des Fühlers plattenartig verschmolzen, Fühler daher nur 1 reihig kammzähnig . . . . **Baria** Karsch, 1896

Typische Art: *B. elsa* (Druce, 1887)

Hierher gehören auch die bisher zu "*Ctenolita*" gestellten Arten ohne Silberzeichnung der Beine.

BESCHREIBUNG DER NEUEN GENERA.

1. **Afraltha** gen. n.

Geschlecht: feminin. Typische Art: *Altha chionostola* Hampson, 1910.

Palpen kurz, aufgebogen, der Stirn angedrückt. Bei den Fühlern des ♂ die Kammzähne plattenartig verschmolzen, Fühler deshalb kurz 1-reihig kammzähnig. Die Kammzähne sind zum Fühlerende hin allmählich verkürzt. Hintertibien mit 2 Spornpaaren, die Mittelsporne weit distalwärts von der Mitte inseriert.

Im Vorderflügel die Vorder- und Hinterecke etwa in gleicher Entfernung vom Aussenrand. Basale Media innerhalb der Mittelzelle scheinbar ungegabelt, da ihre Gabeläste, die sich in wenig spitzem Winkel voneinander entfernen, nach aussen nicht durch eine Querader abgeschlossen sind. r_1 schon vor der Mitte nach vorn convex, an sc herangedrückt. r_2 entspringt kurz vor der Vorderecke der Mittelzelle. r_{3-5} gestielt, r_5 proximal von der Gabelung r_{3+4} entspringend. m_1 ist von diesem Stiel weit getrennt. m_3, cu_1 und cu_2 in immer grösser werdenden Abständen um die Hinterecke der Mittelzelle entspringend, cu_2 mehr distal als r_1.

Im Hinterflügel die Hinterecke der Mittelzelle stark saumwärts vorspringend. Die sc ist in geringer Entfernung von der Flügelwurzel mit dem Vorderrand der Mittelzelle durch Anastomose oder kurze Querader verbunden. $rr + m_1$ sind lang gestielt, m_3 näher cu_1 als m_2; m_2 bis cu_2 frei um die Hinterecke der Mittelzelle entspringend.

Bei der orientalischen Gattung *Altha* Walker, 1862, sind im Hinterflügel rr und m_1 breit getrennt aus der Mittelzelle entspringend, die Fühler des ♂ tragen 2 Reihen von Kammzähnen.

2. **Afrobirthama** gen. n

Geschlecht: feminin. Typische Art: *Narosa flaccidia* Druce, 1899.

Palpen kurz, gerade vorgestreckt oder schwach aufgebogen, ihr Endglied kürzer als $\frac{1}{4}$ des Mittelgliedes. Fühler des ♂ nur in der Basalhälfte mit 2 Reihen von Kammzähnen, in der distalen Hälfte zuerst mit kurzen Sägezäknen, gegen das Ende nackt. Hintertibien mit 2 Spornpaaren, die proximalen weit jenseits der Tibienmitte. Tibien und proximale Tarsenglieder dorsal mit sehr langen Haarschuppen bekleidet. Abdomen dorsal an der Basis mit 2 Schöpfen aus am Ende breit spatelförmig erweiterten Haarschuppen.

Im Vorderflügel die Hinterecke der Mittelzelle stärker saumwärts vorspringend als die Vorderecke. Basale Media in der Mittelzelle kurz gegabelt, vorderer Gabelast schwächer, nur als Falte ausgebildet. r_1 entspringt gegenüber cu_2, verläuft gerade oder nach vorn concav. r_2 entspringt mit den gestielten r_{3-5} aus einem Punkte an der Vorderecke der Mittelzelle, r_5 proximal von der Gabelung r_{3+4} aus dem Stiel. m_1 entspringt weit getrennt vom Stiel r_{3-5}, m_2 bis cu_2 entspringen frei aus der Mittelzelle um deren Hinterecke.

Im Hinterflügel die Hinterecke der Mittelzelle stark saumwärts vorgezogen. Die sc anastomosiert bei $\frac{1}{3}$ des Vorderrandes der Mittelzelle mit ihm; $rr + m_1$ sind gestielt, der Ursprung von m_2 bis cu_2 liegt um die Hinterecke der Mittelzelle, wo diese Adern in etwa gleichen Abständen entspringen.

Bei der orientalischen Gattung *Birthama* Walker, 1862, ist im Vorderflügel der r_1 gleich nach seinem Ursprung stark nach vorn convex, an sc herangedrückt.

Afronarosa gen. n.

Geschlecht: feminin. Typische Art: *Narosa africana* Hering, 1932.

Palpen aufsteigend, Endglied nicht länger als $\frac{1}{4}$ des vorletzten, seine Spitze erreicht, angedrückt, die Höhe des oberen Augenrandes. Fühler des ♀ nackt, lateral-compress, ungewimpert (das ♂ ist noch unbekannt; das als ♂ beschriebene Stück ist ein ♀!), die des ♂ wahrscheinlich auch ohne Kammzähne wie sonst bei den Gattungen mit seitlich zusammengedrückten Fühlern. Nach den Beschreibungen weiterer afrikanischer "*Narosa*", die wohl auch in diese Gattung gehören werden, ist das ebenfalls anzunehmen. Hintertibien mit 2 Paar langen Spornen, das proximale Paar weit jenseits der Tibienmitte.

Im Vorderflügel die Hinterecke der Mittelzelle saumwärts vorspringend. Media in der Mittelzelle ungegabelt erscheinend. r_1 entspringt mehr proximal als cu_2, ist nach dem Ursprung stark convex, an sc herangedrückt. Der r_2 entspringt mit dem Stiel r_{3-5} aus einem Punkt aus der Vorderecke der Mittelzelle. Der r_5 entspringt proximal der Gabelung r_{3+4} aus dem gemeinsamen Stiel. Die m_1 ist von diesem Stiel und von m_2 weit getrennt. Die Ursprünge von m_3 bis cu_1 liegen in etwa gleichen Abständen um die Hinterecke der Mittelzelle, cu_2 weit von cu_1 getrennt.

Im Hinterflügel die Hinterecke der Mittelzelle wenig saumwärts vorragend. sc mit dem Vorderrand der Mittelzelle bei $\frac{1}{3}$ von dessen Länge durch kurze Querader oder Anastomose verbunden. $rr + m_1$ gestielt, m_2 bis cu_2 in etwa gleichen Abständen frei aus der Mittelzelle entspringend.

Bei der orientalischen Gattung *Narosa* Walker, 1855, entspringt im Vorderflügel m_2 stark an m_1 genähert, im Hinterflügel springt die Hinterecke der Mittelzelle sehr stark saumwärts vor.

4. **Jordaniana** gen. n.

Geschlecht: feminin. Typische Art: *Niphadolepis lactea* Pagenstecher, 1903.

Palpen schräg-aufwärts vorgestreckt, ihr Endglied kürzer als $\frac{1}{3}$ des vorletzten, angedrückt bis zum oberen Augenrand reichend, das 2. Glied angedrückt-beschuppt. Fühler bei ♂ und ♀ einfach, ohne Kammzähne, lateral-compress. Hintertibien mit 2 Spornpaaren, die Mittelsporne an der Mitte der Tibia inseriert.

Im Vorderflügel beide Mittelzellen-Ecken in etwa gleicher Entfernung vom Aussenrand. Die basale Media ist rückgebildet, faltenartig, nicht gegabelt erscheinend, da die Gabeläste nach aussen nicht durch eine Querader abgeschlossen sind. Der Ursprung von r_1 liegt proximal von dem von cu_2. Der r_1 ist gerade, nicht an sc herangedrückt. Der Ursprung von r_2 liegt vor der vorderen Zellecke, r_{3-5} entspringen aus der Ecke gestielt, r_5 entspringt proximal von der Gabelung r_{3+4}. m_1 ist von diesem Stiel wie auch von m_2 weit entfernt. Um die hintere Zellecke entspringen m_2 bis cu_1 in etwa gleichen Abständen, cu_2 in wenig grösserem Abstande, alle frei aus der Mittelzelle.

Im Hinterflügel springt die Hinterecke der Mittelzelle stark saumwärts vor. Die sc ist mit dem Vorderrande der Mittelzelle bei dessen Mitte durch eine lange, schräge Querader verbunden. rr + m_1 sind kurz gestielt, m_3 entspringt viel näher cu_1 als m_2.

Bei den habituell ähnlichen *Niphadolepis* Karsch, 1896, ist im Vorderflügel r_1 gleich nach seinem Ursprung stark nach vorn convex, an sc herangebogen.

Benannt zu Ehren des Altmeisters in der Lepidopterologie, Herrn Dr. Karl Jordan (Tring).

5. **Latoiola** gen. n.

Geschlecht: feminin. Typische Art: *Latoia albipuncta* Holland, 1893.

Palpen sehr kurz, gerade vorgestreckt, Endglied unter der Behaarung des 2. verborgen und nicht sichtbar abgesetzt. Fühler bis zur Mitte mit 2 Reihen von Kammzähnen, am Ende nackt. An den Hintertibien fehlen die Mittelsporne, auch die Endsporne sind rückgebildet.

Mittelzelle im Vorderflügel mit stärker saumwärts vorspringender Vorderecke, die basale Media in ihr gegabelt, r_1 entspringt weiter saumwärts als cu_2, ist nur ganz gleichmässig schwach nach vorn convex, nicht an die sc herangebogen. Der Ursprung von r_2 liegt noch vor der vorderen Ecke der Mittelzelle, r_{3-5} entspringen von der Ecke gestielt, wobei r_5 proximal von der Gabelung r_{3+4} aus dem Stiel entspringt. m_1 weit von diesem Stiel wie auch von m_2 entspringend, m_2 und m_3 stark genähert; die Abstände der Ursprünge von m_3 bis cu_2 etwa gleichgross.

Im Hinterflügel springt die Hinterecke der Mittelzelle stark saumwärts vor, die sc mit ihrem Vorderrande noch vor der Mitte durch eine lange Anastomose verbunden. rr + m_1 gestielt, m_2 bis cu_1 in etwa gleichen Abständen um die Hinterecke der Mittelzelle frei aus ihr, cu_2 in etwas grösserem Abstande entspringend.

Bei *Latoia* Guerin, 1844, entspringt im Vorderflügel r_1 in gleicher Höhe mit cu_2 oder proximal davon, die Hinterschienen tragen wohl ausgebildete Endsporne.

6. **Lemuria** gen. n.

Geschlecht: feminin. Typische Art: *Miresa gracilis* Butler, 1882.

Palpen kurz, vorgestreckt, das Endglied kurz, unter der Behaarung des vorletzten nicht sichtbar. Fühler des ♂ bis 2/3 mit 2 Reihen von Kammzähnen. Hintertibien ohne Sporne, zuweilen ein winziger Rest der Endsporne sichtbar (bei der habituell ähnlichen, aber grösseren *Miresa pyrosoma* Butler, 1882, sind 2 deutliche normale Endsporne vorhanden).

Im Vorderflügel die Hinterecke der Mittelzelle nicht saumwärts vorspringend ; in ihr ist die basale Media gegabelt, ihr Vorderast als sklerotisierte Ader ausgebildet. Es entspringen r_1 und cu_2 etwa in gleicher Höhe, r_2 kurz vom Stiel r_{3-5} getrennt aus der Mittelzelle, r_5 proximal von der Gabelung r_{3+4} aus deren Stiel. Die Entfernungen $m_1 - m_2$ und $m_2 - m_3$ sind an den Ursprüngen der Adern etwa gleichgross.

Im Hinterflügel springt die Hinterecke der Mittelzelle wenig saumwärts vor. Die sc anastomosiert nahe der Basis des Flügels mit dem Vorderrand der Mittelzelle. Es sind $rr + m_1$ kurz gestielt, die anderen Adern frei entspringend, Ursprung von m_3 an den von cu_1 genähert.

Bei *Miresa* Walker, 1855, sind in Gegensatz zur vorliegenden Gattung Endsporne der Hintertibien normal ausgebildet, und im Vorderflügel entspringt r_1 saumwärts von cu_2.

7. **Susicina** gen. n.

Geschlecht : feminin. Typische Art : *Susica pyrocausta* Hampson, 1910.

Palpen mässig lang, vorgestreckt ; sie würden, angedrückt, den Oberrand der Augen überragen, ihr Endglied sehr kurz. Fühler beim ♂ lang kammzähnig, beim ♀ kurz sägezähnig ; die letzten 5 Fühlerglieder sind unbewehrt. Hintertibien mit langen Mittel-und Endspornen, die ersten distal von der Tibienmitte inseriert.

Im Vorderflügel die Vorderecke der Mittelzelle saumwärts vorspringend, die basale Media in ihr scheinbar nicht gegabelt, da die Gabelung saumwärts nicht durch eine Querader geschlossen ist. Es entspringen der gerade, nicht nach vorn convexe r_1 gegenüber cu_2, r_2 vor, r_{3-5} von der Vorderecke der Mittelzelle, r_5 proximal von der Gabelung r_{3+4} aus deren Stiel, m_1 von diesem Stiel und von m_2 weit entfernt. m_2 und m_3 sind stärker genähert als die übrigen um die Hinterecke der Mittelzelle frei aus ihr entspringenden Adern.

Im Hinterflügel ist die Hinterecke der Mittelzelle gegen den Saum hin etwas stärker vorgezogen. Die sc ist vor der Mitte des Vorderrandes der Mittelzelle mit ihm durch eine kleine, schräge Querader verbunden. $rr + m_1$ entspringen gestielt, die übrigen Adern frei aus der Mittelzelle, m_2 bis cu_2 in etwa gleichen Abständen um ihre Hinterecke.

Bei der orientalischen Gattung *Susica* Walker, 1855, ist im Vorderflügel die basale Media innerhalb der Mittelzelle lang gegabelt, die Gabeläste nach aussen durch eine Querader geschlossen, und im Hinterflügel springt die Hinterecke der Mittelzelle sehr stark saumwärts vor.

8. **Thoseidea** gen. n.

Geschlecht : feminin. Typische Art : *Thosea lineapunctata* Bethune-Baker, 1911.

Palpen mässig lang, vorgestreckt, das Endglied etwas hängend. Fühler des ♂ nur im Basaldrittel mit 2 Reihen langer Kammzähne. Hintertibien mit 2 Paaren von Spornen.

Im Vorderflügel die Vorderecke der Mittelzelle stärker vorgezogen, die basale Media in der Mittelzelle scheinbar nicht gegabelt. Es entspringen r_1 weit saumwärts von cu_2, r_{2-5} gestielt, aus diesem Stiel r_2 erst distal von r_5, r_{3+4} zuletzt gegabelt, m_1 weit von m_2 entfernt, m_2 bis cu_1 etwa in gleicher Entfernung um die Hinterecke der Mittelzelle.

Im Hinterflügel springt die Hinterecke der Mittelzelle stark saumwärts vor, die sc anastomosiert mit ihrem Vorderrand nahe der Flügelwurzel. $rr + m_1$ sind kurz gestielt, die übrigen entspringen frei aus der Mittelzelle, m_3 bis cu_1 in etwa gleichen Abständen um deren Hinterecke.

Bei der zum Teil orientalischen Gattung *Thosea* Walker, 1855, entspringt r_2 proximal von r_5 aus dem Stiel r_{3+4} im Vorderflügel, oder sie kommt auch frei aus der Mittelzelle. Von afrikanischen Arten gehört *Th. serrata* Hering, 1928, zur echten *Thosea* Walker, *Th. perseis* Fawcett, 1917, zu *Thoseidea* Hering.

9. **Xanthopteryx** gen. n.

Geschlecht: feminin. Typische Art: *Susica confusa* Walker, 1865.

Palpen mässig gross, vorgestreckt, ihr Endglied deutlich abgesetzt, aber nur $\frac{1}{4}$ des vorletzten lang. Fühler des ♂ bis $\frac{2}{3}$ oder $\frac{3}{4}$ mit 2 Reihen von langen Kammzähnen, Endviertel in den letzten bis zu 20 Segmenten mit nur 1 Reihe von kurzen Sägezähnen. Hintertibien mit 2 langen Spornpaaren, Mittelsporne etwas distal von der Tibienmitte inseriert.

Im Vorderflügel Vorder-und Hinterecke der Mittelzelle etwa auf gleicher Höhe. Basale Media in der Mittelzelle lang gegabelt, Gabelung etwa gegenüber dem Ursprung von r_1, dieser wenig proximal von dem von cu_2. Es entspringen r_2 und r_5 aus einem Punkt mit dem Stiel r_{3+4} aus der Mittelzelle, m_1 weit von r_5 und m_2 entfernt, m_2 bis cu_1 in etwa gleichen Abständen um die Hinterecke der Mittelzelle.

Im Hinterflügel die Hinterecke der Mittelzelle stark saumwärts vorspringend, so weit distal von der Mitte des Mittelzellen-Vorderrandes mit ihm durch eine lange, schräge Querader verbunden. $rr + m_1$ gestielt, die übrigen Adern frei aus der Mittelzelle, m_2 weiter von m_3 als diese von cu_1 entfernt, die Ursprungsentfernung $cu_1 - cu_2$ noch grösser.

Bei den orientalischen *Susica* Walker, 1855, ist die Hinterecke der Mittelzelle im Vorderflügel deutlicher saumwärts vorgezogen, r_2 entspringt vor dem Zellende, r_5 ist mit r_{3+4} deutlich gestielt; im Hinterflügel liegt die Verbindung der sc mit dem Mittelzellen-Vorderrand vor dessen Mitte.

"It would almost appear, in fact, as if a 'species' is that which a respective author chooses to consider a 'species'."

(Jordan, K., 1896, *Novit. zool.* **3** : 426.)

ON THE TAXONOMIC POSITION OF THE ACROLOPHINAE, WITH A DESCRIPTION OF THE LARVA OF *ACROLOPHUS RUPESTRIS* WALSINGHAM (LEPIDOPTERA : TINEIDAE).

By H. E. Hinton.

(*Department of Zoology, University of Bristol.*)

With 12 Text-figures

It has often been the practice to include in the Tineidae microlepidoptera the affinities of which seemed to be in doubt. Even so well known an authority as Meyrick has placed in the genus *Tinea* L. not only species which are congeneric with the type species, *T. pellionella* L., but also species which belong to the Incurvaroidea. For instance, *Tinea nectarea* Meyrick (1893, *Proc. linn. Soc. N. S. W.* **17** : 546), the larva of which I have recently examined, not only does not belong to the family Tineidae but belongs to another suborder, the Monotrysia. Meyrick has thus placed in the same genus species belonging to two different suborders, the Monotrysia and Ditrysia. In the check list of Kloet and Hincks (1945) various primitive Psychidae, such as *Taleporia* Hübner, *Solenobia* Duponchel, *Luffia* Tutt and *Narycia* Stephens, are included in the Tineidae as is *Ochsenheimeria* Hübner, the type of an unrelated family, the Ochsenheimeriidae.

The Acrolophinae are confined to America, where most of the species are Neotropical. The principal genus is *Acrolophus* Poey. The systematic position of the group is much disputed. Most writers have placed it in the family Tineidae, but some have held that it belonged in the family Psychidae. A new family, the Acrolophidae, was erected by Dyar (1902) to contain *Acrolophus* and related genera. In his work on the chaetotaxy of lepidopterous larvae, Fracker (1915) described the larva of *Acrolophus arcanellus* Clemens and followed Dyar in retaining the group as a distinct family. Fracker drew attention to the multiserial circle of crochets on the prolegs, and, in addition, claimed that the Acrolophinae could be distinguished from the Tineidae by the arrangement of the L setal group on the prothorax. L1 is nearest to the spiracle and nearer to L3 than to L2. However, this distinction cannot be confirmed in a number of Tineid larvae recently examined by me. For instance, in *Monopis congestrella* Walker and some species of *Amydria* Clemens L1 is nearly as close to the spiracle as is L3, and in *Nemapogon parasitella* Hübner L1 is nearer to the spiracle than either L2 or L3. It may not be necessary to add that *Monopis*, *Amydria*, and *Nemapogon* are typical Tineidae. It may be noted here that in his maps of the chaetotaxy Fracker has omitted setae MD1, MSD1, MSD2, MV2, and MV3 on the prothorax, MD1 and all MV setae on the mesothorax, and both MD1 and MV3 on the abdomen. Forbes (1923) considered *Acrolophus* and related genera to be no more than a subfamily within the Tineidae, and this is my own view. More recently, Costa Lima (1945) has again given the Acrolophinae family rank.

I have been able to examine only the larva of *Acrolophus rupestris* Walsingham of Jamaica (figs. 1–12). The chaetotaxy of this larva is characteristic of that of the family Tineidae. Only in one respect does *Acrolophus* differ from all other Tineidae known to me: the postgenae (fig. 3) are nearly fused together on a broad front along the median line. It is true that each proleg of segments three to six and ten has a broad band of recurved spines or small crochets above the usual crochets, as shown in fig. 6, but similar bands of small crochets are present on each proleg of segments three to six but not ten of some Tineidae examined by me, e.g. *Lindera* Blanchard and *Setomorpha* Zeller.

On their structural features the larvae of the Tineidae may be placed in four subfamilies: Acrolophinae, Scardinae, Nemapogoninae, and Tineinae. Such a division is partly supported by the feeding habits of the larvae. The Acrolophinae live in silken galleries and webs in the ground, and are known to feed on clover and on the roots of grasses. The Scardinae feed upon fungi. The Nemapogoninae feed principally upon fungi in or on decaying wood, and a few species attack stored vegetable products, especially when these are mouldy. The Tineinae normally feed upon more or less dry animal matter, especially hair and feathers, and they seem to be the only group in the family capable of splitting disulphide bonds. A key to the subfamilies is as follows:

1. Head with postgenae nearly fused together on a broad front along median line (fig. 3). Prolegs of segments three to six and ten each with a broad band of recurved spines or smaller crochets above the usual crochets (figs. 5–6). SV setal group of meso- (fig. 7) and metathorax unisetose . . . . **Acrolophinae** (*Acrolophus*).

– Head with postgenae only near each other on a very narrow front. Prolegs without recurved spines above crochets except in *Lindera* and *Setomorpha* in which such spines are present above the crochets of prolegs of segments three to six, but not above those of prolegs of tenth segment 2

2. L group of prothorax bisetose. D1 setae on first eight abdominal segments more widely separated than D2 setae **Scardinae** (*Scardia*, *Morophaga*).

– L group of prothorax trisetose. D1 setae of first eight abdominal segments less widely separated than D2 setae 3

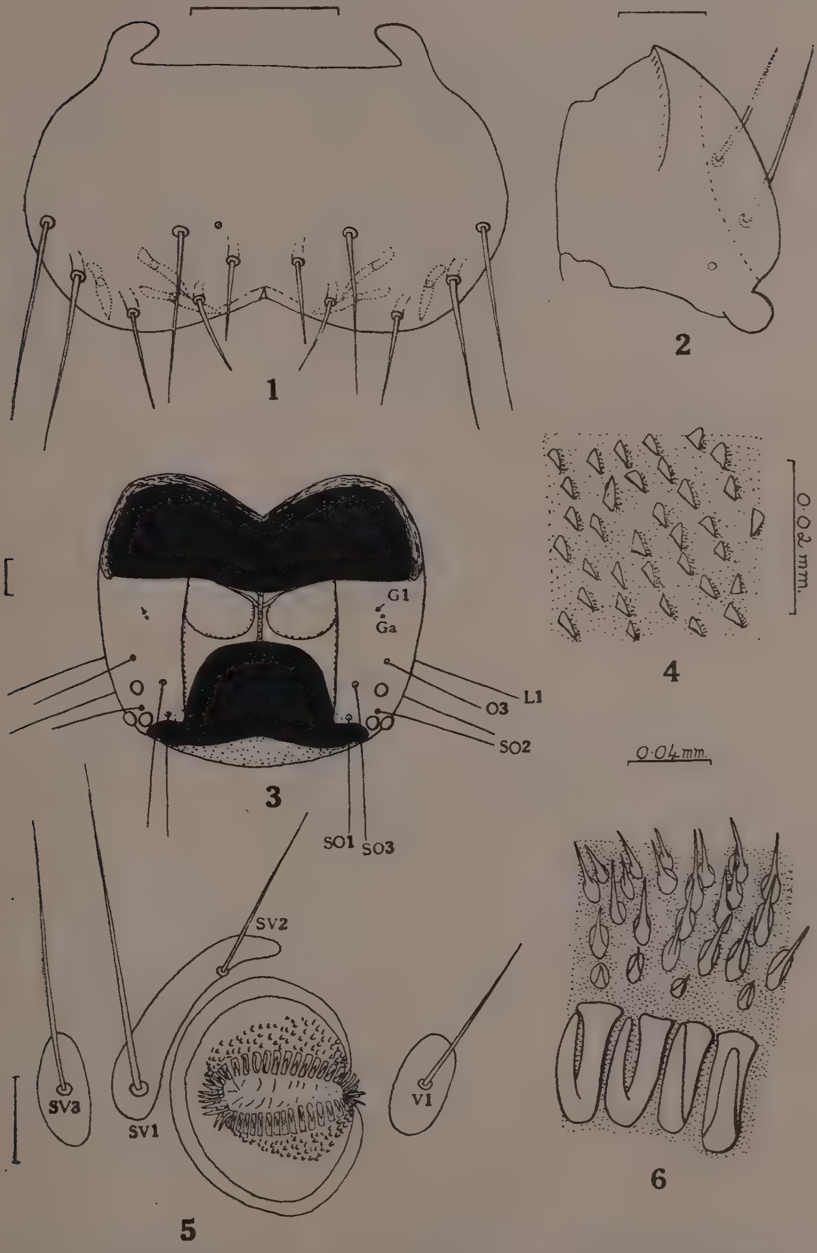
3. SV group of meso- and metathorax unisetose. Head usually with five or six convex ocellar lenses on each side but sometimes with less than five or none **Nemapogoninae** (*Nemapogon*, *Lindera*, *Setomorpha*).

– SV group of meso- and metathorax bisetose. Head never with more than a single convex ocellar lens on each side **Tineinae** (*Tinea*, *Acedes*, *Tineola*, *Amydria*, *Monopis*, *Trichophaga*).

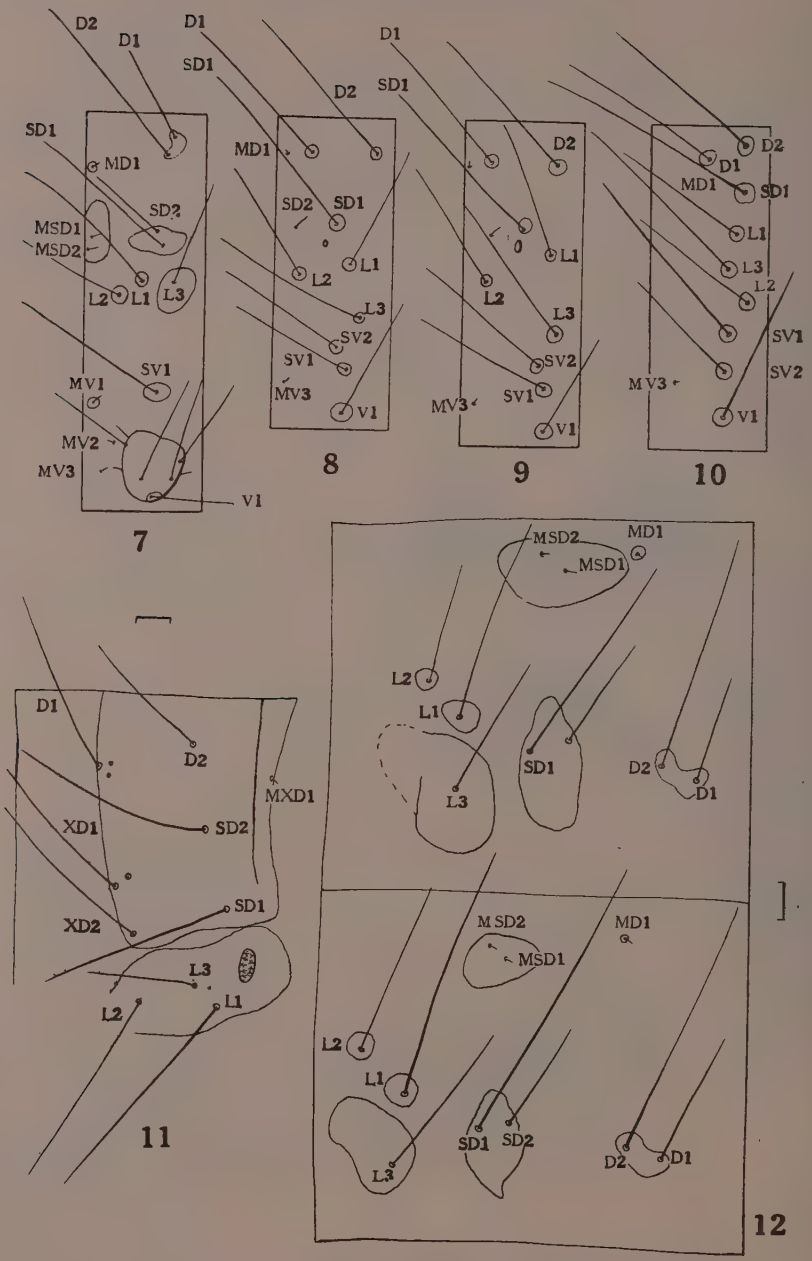
The larva of *Acrolophus rupestris* Walsingham.

The terminology of the cranial areas is that of Hinton (1948), and the terminology of the setae is that of Hinton (1946).

Mature larva.—Length, 26 mm.; breadth, 4 mm. Head dark brown; tergum and pleural plates of prothorax paler brown; legs yellowish; peritreme of spiracles dark brown to nearly black; body elsewhere whitish with tergum of tenth abdominal segment darker. Head with part of fronto-clypeal apotome enclosed by adfrontal sutures extending distinctly less than half of distance to vertical triangle. Six ocellar lenses on each side. Coxae of all legs moderately widely separated. Spiracles oblong-oval, eighth abdominal segment with spiracles more than twice as long as those of seventh (7 : 3) and equal in size to those of prothorax. *Chaetotaxy:* AF1 nearer to F1 than to AFa; AFa nearer to AF2 than to AF1 and slightly above the level of the apparent junction of adfrontal sutures. Va in a


1
2
G1
Ga
L1
O3
SO2
0·02 mm.
4
0·04 mm.
3
SO1
SO3
SV2
SV3
SV1
V1
5
6

Figs. 1–6.—Larva of *Acrolophus rupestris* Walsingham. (1) Dorsal view of labrum. (2) Ventro-mesal view of left mandible. (3) Ventral view of cranium. (4) Microsculpture of the cuticle as illustrated by that of the eighth abdominal segment. (5) Ventral view of first proleg of right side. (6) Crochets and a section of the recurved spines below the crochets of the same proleg.


D2
D1
SD1
MD1
SD2
MSD1
MSD2
L2
L1
L3
SV1
MV1
MV2
MV3
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7
D1
SD1
D2
MD1
SD2
SD1
L1
L2
L3
SV2
SV1
MV3
V1
8
D1
SD1
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M SD2
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L3
12

FIGS. 7–12.—Larva of *Acrolophus rupestris* Walsingham. (7) Setal map of left side of mesothorax. (8) Same of seventh abdominal segment. (9) Same of eighth abdominal segment. (10) Same of ninth abdominal segment. (11) Setal map of tergum and pleurum of left side of prothorax. (12) Same of meso- and metathorax. Lines next to all figs. refer to 0·20 mm. unless otherwise indicated.

nearly straight line with, and half way between, V3 and V2. P2 almost directly laterad from P1 ; Pa directly behind P1 and almost directly mesad from V1. Aa slightly nearer to A2 than to A3, and in a nearly straight line between these setae. G and SO setal groups as shown in fig. 3. Chaetotaxy of prothorax (fig. 11), meso- and metathorax (figs. 7 and 12), first eight abdominal segments (figs. 8–9), and ninth abdominal segment (fig. 10) as illustrated.

Comparative notes.—The setae are much longer than those illustrated by Fracker (1915) for *A. arcanellus* Clem., most of them being considerably longer than their respective segments. In *A. arcanellus* L3 of the prothorax is as far from L1 as it is from L2, whereas in *A. rupestris* L3 is only half as far from L1 as it is from L2 (fig. 11).

ACKNOWLEDGMENTS.

I am indebted to Mr. J. F. Gates Clarke for the gift of a larva of *Setomorpha rutella* Zeller and to Mr. J. D. Bradley for his assistance with some of the literature.

SUMMARY.

A number of genera sometimes placed in the Tineidae are removed to other families. It is shown that the structure of the larva of *Acrolophus* supports the view that the Acrolophinae should be included in the Tineidae. A key is given to the larvae of the subfamilies of Tineidae. The larva of *Acrolophus rupestris* Walsingham is described.

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“A satisfactory insight into the true connection between the members of any group of animals will not be gained, unless the classifier takes as his aim to ascertain, so far as that is possible from the necessarily incomplete knowledge of the organs, the probable phyletic development of each single distinguishing character, so that we get a picture of the gradual modification of the various organs from the ancestral stage of development into those stages of mutation which we now observe in the different members of the group to be classified.”

(Jordan, K., 1898, *Novit. zool.* **5** : 399.)

PRIMARY AND SECONDARY SEXUAL CHARACTERISTICS OF SOME CERATOPHYLLINAE, WITH NOTES ON THE MECHANISM OF COPULATION (SIPHONAPTERA).[1]

By George P. Holland.
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With 13 Text-figures.

Introduction.

Although the systematics and disease-transmitting propensities of fleas have been studied intensively, relatively little is known of the life-histories and habits of these insects except for a few species, and, with these, certain particulars remain obscure. In this category is the method whereby copulation and fertilisation are accomplished.

There is very little literature on this subject. Of the few publications available, those of Mitzmain (1910), Waterston (1912) and Lundblad (1926) provide the most important original observations on these phenomena in the living insect. These authors described the mating act, in varying detail, as observed in *Ceratophyllus acutus* Baker [*Diamanus montanus* (Baker)], *Ceratophyllus farreni* Rothschild, and *Ceratophyllus gallinae* (Schrank), respectively. Mitzmain and Waterston, although working at times only with hand lenses, provided some exceedingly detailed notes on the mating behaviour, describing the positions adopted by the male and female during coitus, as well as the relationships of some of the anatomical parts. Mitzmain and Lundblad independently observed and reported the rôle of the antennae of the male.

Snodgrass, in his important paper on the skeletal anatomy of fleas (1946), included an explanation of the morphology of the male genitalia of several species, and described the relations of the intromittent organ from a slide preparation of a mated pair of *Ceratophyllus* [*rossittensis*] *swansoni* Liu. He did not discuss in any detail the relationships of the claspers and other structures of the genitalia in the mating act, but, writing of the aedeagus and related structures, remarked, " It is hard to imagine why a male insect should need, for the mere transfer of sperm to the female, an organ so elaborate in structure and so complex in its mechanism as is the intromittent apparatus of the fleas ; and it can only be inferred from the structure of the organ how the latter accomplishes its purpose ".

The present writer is not able to resolve all of the many mysteries that remain. However, an examination of a few specimens of fleas *in cop.* has revealed a number of facts that corroborate, supplement, or in some cases contradict, the observations of earlier authors. The present paper, then, summarises the available information.

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[1] Contribution No. 3293, Entomology Division, Science Service, Department of Agriculture, Ottawa, Canada.

MATERIALS AND METHODS.

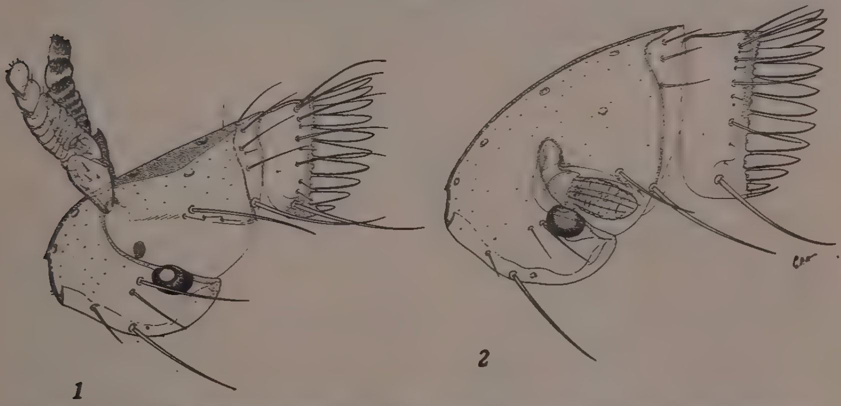
A major difficulty has been that of obtaining suitable preparations for study. Although freshly emerged fleas of several species were found to mate fairly freely in the laboratory, it was often difficult to kill them without the individuals becoming partially or wholly separated during their dying struggles. Waterston (1912) tried several systems, including anaesthetisation and decapitation with a sharp razor, with varying success. The present writer also tried a number of methods, and found two that were reasonably reliable. In the first, a mating pair of fleas in a plugged glass tube was placed in a refrigerator (set at approximately 34° F.) for about twenty minutes. The fleas became torpid, but did not release their clasp. They were then dropped quickly into liquid chloroform. In the second and simpler method, the copulating specimens were dropped into boiling water. Specimens were preserved in 70 per cent. alcohol until prepared as slide mounts. The technique for preparation was the standard KOH-water-alcohol-oil of wintergreen-Canada balsam procedure (e.g., Holland, 1949) except that the fluids were added or drawn off with a pipette instead of transferring the specimens (with risk of separation) from vessel to vessel. At the final stage, the fleas were lifted carefully upon a spatula and transferred to a drop of balsam on a slide. Despite all precautions, some of the specimens came adrift in the mounting procedure. However, the technique yielded a number of preparations in which the relationships of the genital parts could readily be discerned. It had the undesirable feature that the position of the male beneath the female became altered, so that in a finished preparation the specimens, though still joined posteriorly, were at an angle to each other rather than parallel, one beneath the other. In two instances it was possible to obtain specimens in approximately natural position by carrying out the chemical treatment in a vessel that contained a half-inch layer of paraffin wax on which the specimens were held in position by several slender entomological pins.

By means of the above procedures, and through loans of material from other institutions, the writer has been able to study slide preparations of varying quality of 23 mated pairs of fleas as follows: *Ceratophyllus idius* Jordan & Rothschild, 16 pairs; *C. niger* Fox, 1 pair; *C. farreni* Rothschild, 2 pairs; *C. rossittensis swansoni* Liu, 1 pair (Snodgrass' specimen); *Monopsyllus wagneri* (Baker), 1 pair; and *Diamanus montanus* (Baker), 2 pairs. All of these species belong to the Ceratophyllinae of the Ceratophyllidae, and all but *D. montanus* belong to the tribe Ceratophyllini. As the publications of the previous authors mentioned all deal with species of *Ceratophyllus* or *Diamanus*, the information now available is limited in scope and possibly of application, for although the genital apparatus of female fleas is of more or less "standard pattern" throughout the order (excepting the few species possessing paired spermathecae), the genitalia of male fleas may differ widely in various families. Though the fundamental method of accomplishing coitus may be similar throughout the order, details may differ so that a function performed by a structure in one species may be performed by a different structure in another. The descriptions and discussions that follow, then, pertain to some Ceratophyllinae only; it is hoped that opportunities will occur to make similar observations on copulating fleas belonging to other families.

ANATOMICAL NOTES.

The following account deals principally with primary and secondary sexual structures, and is intended merely as a basis for a discussion of the act of copulation.

In the Ceratophyllinae, as with many fleas, there is strong sexual dimorphism aside from genitalic differences, the males being smaller than the females, differently shaped in profile, and with longer antennae. The dorsum (head, thorax and abdomen) of the male is usually straight, or even somewhat concave, whereas that of the female is more or less convex.



FIGS. 1, 2.—*Diamanus montanus* (Baker). Sexual dimorphism in head and pronotum (1) Male. (2) Female.

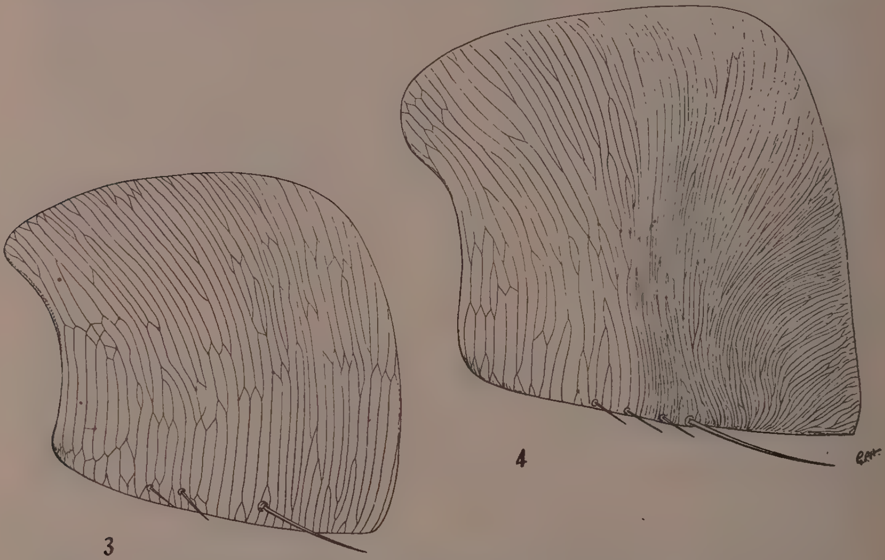
Head.—The dorsum of the head of the male, in profile, is almost flat, and possesses a longitudinal groove (fig. 1), whereas the female head is more rounded and lacks such a groove (fig. 2). The antennae of the female are short, not strongly erectile, and with the club more or less round in cross section. They originate on the sides of the head, and the apex of the club does not usually extend beyond the margin of the head. In the males, the antennae, which originate at the vertex, are much longer, and in the retracted condition frequently extend well beyond the hind margin of the head. They are strongly erectile, with the club flattened in cross-section and its inner surface densely hirsute with short fine setae. The development of the marginal setae of the second antennal segment frequently differs in the sexes, those of the female usually being longer, or at least proportionately longer. In *Diamanus montanus* these setae are extremely short in the male, but exceed the length of the club in the female. However, the males of most *Ceratophyllus* spp. have these setae long, though not quite so long as in the female.

Thorax.—The thorax does not appear to possess any significant secondary sexual characters, although there may be minor differences in chaetotaxy and the pronotal comb of the female sometimes contains more spines than that of the male. The sexual significance of this feature, if any, is not apparent.

Anterior abdominal segments.—The first six abdominal segments are relatively unmodified except for the absence of sternum I, and the overlapping of tergum II by sternum II instead of the reverse, as in segments III–VI.

There are no conspicuous sexual differences, although the writer has observed in several species a difference in the surface markings of the basal abdominal sternum (St. II) that may have a sexual significance (figs. 3 and 4).

Abdominal segment VII.—In the female, segment VII is of similar size to the preceding segments, but differs in that the sternum overlaps the tergum, instead of the reverse. The tergum, too, bears dorsally on each side a group of strong marginal setae termed the antepygidial bristles; it lacks the apical spinelets that are to be found on some of the "unmodified" abdominal terga of all ceratophyllines. The apical margin of sternum VII may be "entire" (thus resembling the anterior sterna) or it may be developed into lobes and sinuses that are usually of distinctive form in different species.



Figs. 3, 4.—*Ceratophyllus idius* Jordan & Rothschild. Sexual dimorphism in surface striations of abdominal sternum II. (3) Male. (4) Female.

In the male, the tergum overlaps the sternum in normal fashion. Antepygidial bristles are present but usually fewer in number than in the female, or, if of the same number, some of them are much shorter than those of the female. The apical margin of sternum VII is virtually unmodified, but may be dilated slightly to enclose the base of sternum VIII.

Abdominal segment VIII.—In both males and females of Ceratophyllinae, tergum VIII is expanded into a broad pair of rounded valves that almost enclose the external genitalia. It differs from those of segments I–VII (as in all fleas) in the location of its spiracles, which open inside the dorsal margin beside the sensilium or pygidium (figs. 5 and 6) rather than laterally on the sclerite. Tergum VIII lacks marginal spines, but bears a characteristic vestiture of lateral and marginal setae. In the males there is frequently a dense patch of spinelets on the inner dorsal surface. Females have several stout setae on the mesal surface near the postero-ventral margin.

Sternum VIII in the female is reduced, weakly sclerotised, and usually entirely contained within the ventral margins of tergum VIII, although in some fleas its ventral margin, and perhaps its apex, may protrude slightly.

Although in the males of some Ceratophyllinae sternum VIII is vestigial, being reduced to a small, inconspicuous structure, in most species, including all of those under consideration, it is modified into a long, rod-like structure with apical setae, and sometimes with apical membranous appendages ; this rod fills the space between the ventral margins of the " valves " of tergum VIII. Proximally, on each side, a small triangular portion is all that remains to represent the lateral elements of the sclerite. Associated with these are a pair of small, rounded organs of uncertain function, termed the " glands of Wagner ".

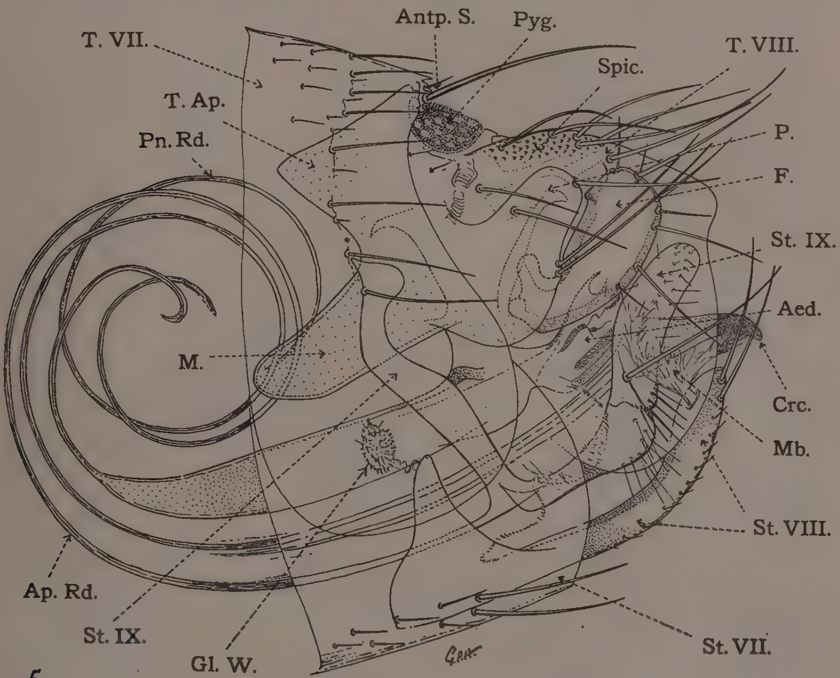


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Fig. 5.—*C. idius.* Terminal abdominal segments and genitalia of male. *Aed.*, aedeagus ; *Antp.S.*, antepygidial setae ; *Ap.Rd.*, apodemal rod of sternum IX ; *Crc.*, crochet ; *F.*, movable process of clasper ; *Gl.W.*, gland of Wagner ; *M.*, manubrium ; *Mb.*, membranous appendage of sternum VIII ; *P.*, fixed process ; *Pn.Rd.*, penis rod ; *Pyg.*, sensilium (= pygidium) ; *Spic.*, spiculose area of tergum VIII ; *St.*, sternum ; *T.*, tergum ; *T.Ap.*, tergal apodeme of segment IX.

Abdominal segment IX.—As Snodgrass states (1946 : 36), ". . . in most female fleas it (i.e. segment IX) is practically obliterated ". Although nothing of the tergum can be observed, the membranous ninth sternum, frequently bearing pale setae, can be seen in many Ceratophyllinae, the genital opening lying between this and sternum VIII.

The elements of the male segment IX are manifested very differently in different groups of fleas. In the Ceratophyllinae, the tergum proper can hardly be observed, being " . . . reduced to a narrow strip over the back . . . a mere line on which are attached the conjunctiva from tergum VIII and that to segment X" (Snodgrass, 1946 : 38). Fused with it on either side, and apparently derived from it, is a tergal apodeme which is in turn fused with a clasper lobe, bearing anteriorly a manubrium and posteriorly the claspers proper, the latter composed (in Ceratophyllinae) of a fixed and a movable process, the shape and armature of which are of the greatest taxonomic significance. The movable process articulates mesally in an acetabulum, that is guarded externally by acetabular setae. Muscles operate to control movement so that the movable process can be brought against the fixed process like a pair of pincers. At the point of contact, the movable process usually bears a small tubercle which engages in a hollow or groove on the inner side of the apex of the fixed process. Although much has been written about these " claspers ",

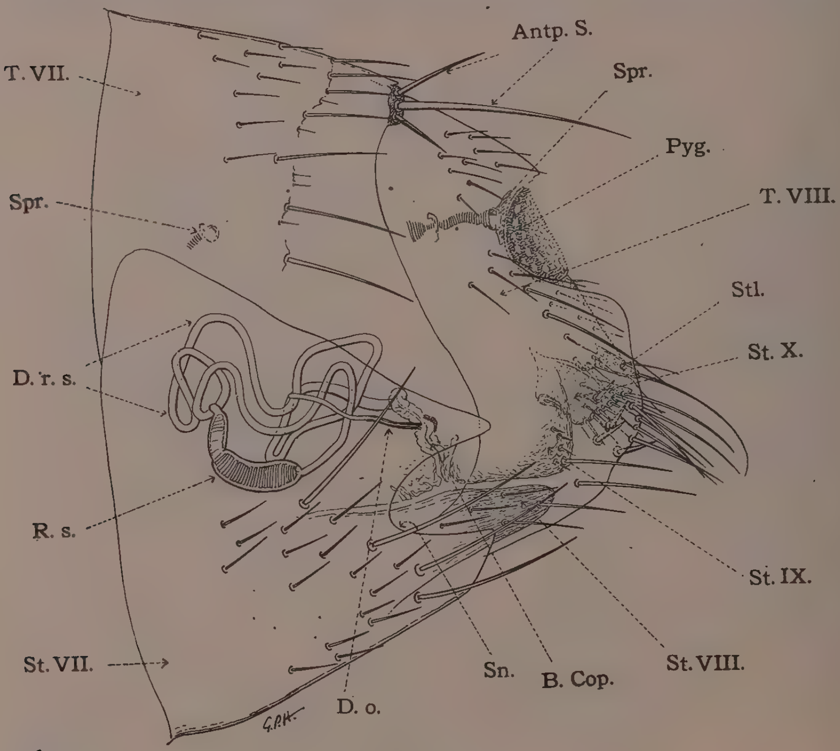

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Fig. 6.—*C. idius.* Terminal abdominal segments and genitalia of female. *Antp.S.*, antepygidial setae ; *B.Cop.*, bursa copulatrix ; *D.o.*, ductus obturatus ; *D.r.s.*, ductus receptaculi seminis ; *Pyg.*, sensilium ; *R.s.*, spermatheca (receptaculum seminis) ; *Sn.*, sinus of sternum VII ; *Spr.*, spiracle ; *St.*, sternum ; *Stl.*, anal stylet ; *T.*, tergum.

the writer is not aware of any published observations on what it is they are supposed to "clasp" although some authors have presumed (correctly) that the seventh sternum of the female is seized by them.

Sternum IX varies greatly in different groups of fleas, but attains its greatest complexity, perhaps, in the Ceratophyllinae. Viewed laterally, each half of the sclerite appears as a boomerang-shaped structure, with a simple proximal (dorsal) arm, which is usually somewhat curved, and a complex distal (ventral) arm. At their juncture, and the juncture of the two halves of the sternum, is an apodemal rod that extends forward as part of the skeletal support of the endophallus. The distal arm of sternum IX lies over the manubrium of the clasper, i.e. the sternum overlaps the tergum in segment IX. In many Ceratophyllinae there are elaborate intersegmental membranous lobes of possible sensory function (e.g., Wagner, 1932, 1933) connecting sterna VIII and IX.

Abdominal segment X.—Segment X of fleas, male or female, is represented by a sensory plate, the sensilium (often termed pygidium) and the proctiger. The sensilium contains a number of pits, each bearing a long sensory hair (trichobothria, according to Lundblad, 1926 : 22); its precise function is not known. The sensilium of the female is somewhat larger than that of the male. In most fleas, including those under consideration in this paper, the dorsal flap of the proctiger of the female bears on each side an "anal stylet", which usually terminates apically in a long seta. The ventral margin of sternum X of the female bears a row of long, stout setae. The proctiger of the male lacks a stylet, but is beset with slender setae.

Intromittent organ of the male.—The intromittent organ of fleas, consisting of an external aedeagus (or phallosome) and an internal endophallus, has been discussed in varying detail by Jordan (1939), Sharif (1945), Snodgrass (1946), Traub (1950) and Hopkins and Rothschild (1953). Of concern in the present paper are the aedeagus, which may have characteristic lobes and a pair of crochets (not parameres), and the penis rods, which in the act of copulation are protracted through the inner tube of the aedeagus. As Snodgrass points out (1946 : 68), the penis proper of fleas is not protracted, and the gonopore is located within the endophallus; spermatozoa are therefore transferred to the penis rods, which ". . . are the only elements of the intromittent apparatus that are capable of being protracted from the aedeagus, and they alone enter the bursa copulatrix of the female".

Female genitalia.—The female genital chamber is contained within the postero-ventral areas of tergum VIII, below the proctiger. The vagina is bordered by the sterna of segments VIII and IX. At the proximal end of the vagina is the gonopore, or mouth of the median oviduct, and immediately above it is an opening leading to the sperm-receiving organs (fig. 6). This opening leads by a short duct to the bursa copulatrix, which, in Ceratophyllidae, is a relatively simple tube receiving two ducts. The major duct, which is long and convoluted in the species of *Ceratophyllus* under consideration (shorter in others), leads directly to the spermatheca, or receptaculum seminis, a flask-shaped organ with a head and tail section. The second duct, the ductus obturatus, is blind; its basal portion may be heavily sclerotised, and in the wall of the bursa copulatrix opposite the entrance to this duct there may be a small sclerotised thickening. In a few species of fleas there are two sperma-

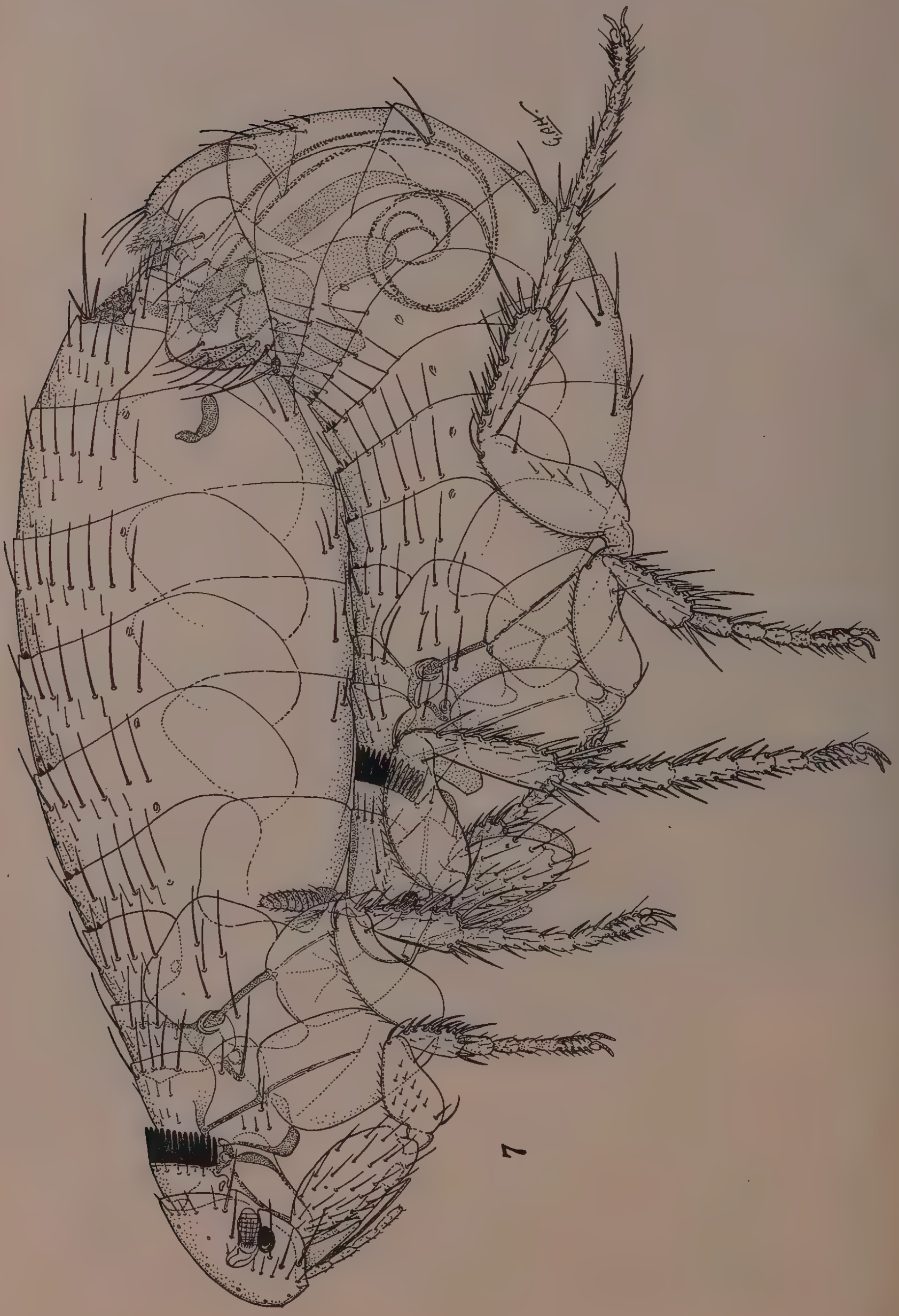


FIG. 7.—*C. idius.* Male and female *in copula*; a composite drawing, based on several preparations.

thecae, each with a duct, and this has been presumed to represent the primitive condition (e.g., Jordan, 1921). In fleas bearing one spermatheca, the blind duct, when present, has been interpreted as a vestige of the tube of the lost spermatheca. Two species of fleas, *Macropsylla hercules* Rothschild and *Atyphloceras shogakii* Jameson & Sakag., possess unequal spermathecae, suggesting an evolutionary stage leading to the loss of one of these organs.

MATING BEHAVIOUR AND THE RELATIONS OF THE SEX ORGANS AND ACCESSORY STRUCTURES DURING COPULATION.

The mating act in fleas, as exemplified by specimens of several species of Ceratophyllidae, may be considered as a succession of steps :

(1) *Attack by the male.*—Mitzmain (1910) and others are agreed that the male flea is the agressor, carrying the attack to the female, although once engaged in copulation he appears to play a relatively passive rôle. According to Waterston (1912 : 79) copulation (in *C. farreni*) " is the first business of the imaginal state ", although Mitzmain, writing of *Diamanus montanus*, found that a blood meal was necessary before the fleas could be induced to mate. Poole and Underhill (1953), in discussing *Megabothris c. clantoni* Hubbard, stated that a blood meal was prerequisite, and further that females ". . . fed on mice . . . for the first time would not copulate until the next day ". It seems probable, then, that the habits of species vary in this respect, although laboratory conditions may have influenced the behaviour of the fleas studied.

On several occasions in the laboratory, the present writer observed freshly emerged males of *Ceratophyllus niger* Fox, *C. idius* Jordan & Rothschild and *C. riparius* Rothschild to mate with unfed females. In one instance a male of *C. niger* was seen to mate within 60 seconds of emerging from his cocoon ! The males of all three species would approach females, and, in the manner reported by earlier authors, dart beneath them, elevating their antennae so that they were erect, like a pair of horns (hence " Ceratophyllus ") and firmly clasp the basal abdominal sternum. The union of the head of the male to the venter of the female in these and many other species is facilitated by the presence of the longitudinal groove on the head (figs. 1 and 7) into which the sternum fits. As pointed out by Lundblad (1926), the male antennae are flat and hairy on their inner surfaces, an undoubted adaptation to their clasping function. This suggested to the present writer that a comparison should be made of the basal abdominal sterna of male and female fleas to ascertain whether the latter possessed any special modifications to facilitate clasping by the male antennae. It was found that frequently in *Ceratophyllus* and related genera the surface striations of that sclerite were more numerous in the female, and that they ran at an angle or in a direction that appeared advantageous to the presumed purpose, whereas those of the male did not (e.g., figs 3 and 4).

In some fleas, notably the Neopsyllinae and some Rhadinopsyllinae, there may be a dense patch of striae, either on sternum II or on the metepimere (e.g., Holland, 1949, figs. 63 and 97). Species of fleas having such a " striarium " usually possess also a patch of spiniforms or stiff setae on the inside of the hind coxae. Enderlein (1930) claimed that in *Pulex irritans* L. the spiniforms and striae operate as a stridulating apparatus, although Jordan (1947) questioned such a possibility, stating that in some species at least it would be a physical impossibility for the coxae to be elevated sufficiently for the spines to come in contact with the striae. An alternative explanation for such structures, then, might be that the striae of females constitute gripping areas for the male antennae during copulation, and the spinelets of the coxae, by pressure on the sides of the head of the male, assist in holding it in position. An objectionable feature is that in species characterised by the presence of a striarium the structure is present in both sexes, whereas if it were a secondary sexual modification one would expect it to be absent from the male, or at least especially well developed in the female. Some species (e.g., *Odontopsyllus* spp. and *Nearctopsylla* spp.) possess spiniform setae on the hind coxae, but lack a patch of modified striae. The writer was unable to observe whether the coxae of the females exerted pressure on the heads of the males in the species studied, although Mitzmain (1910 : 68) suggested that it is the hind femora rather than the coxae that grip the head ; this feature, of course, may differ in species.

Having seized the female by his erected antennae, the male flea would then elevate his abdomen, telescoping the terga somewhat (fig. 7) so that his dorsum conformed to the contour of the venter of her abdomen, and the mating clasp was then accomplished by the terminalia. The writer made but few observations on the living insects *in cop.* as his main purpose was to kill them so as to make preparations that would reveal the relationships of the various structures. Nonetheless, the actions of the fleas were found to conform closely with the statements of Mitzmain and Waterston, who described the phenomena in considerable detail.

Once the fleas were paired, the male became relatively passive, remaining closely suspended beneath the female by means of antennae anteriorly and genitalia posteriorly. The paired fleas appeared and acted like a single insect, the male was so well hidden beneath the female. In lateral view, too, the two appeared as one, a line running around the dorsum of the female continuing around the venter of the male in one unbroken contour (fig. 7). The paired fleas moved about freely, the female providing the means of locomotion.

Copulation sometimes takes place on the host animal, and sometimes in the nest. It may be that species vary in this respect, or that in general they mate indiscriminately, wherever they find partners ; there are few data. The writer has observed specimens of *Thrassis acamantis* (Rothschild) and *Monopsyllus wagneri* (Baker) mating on their hosts, *Marmota flaviventris avara* (Bangs), in April, and *Peromyscus maniculatus artemisiae* (Rhoads), in August, respectively, but has only observed the bird fleas, *Ceratophyllus* spp., breeding in the nests of their hosts (*C. niger* in August ; *C. idius* and *C. riparius* in September).

(2) *Union of the terminalia.*—Union of the terminalia is achieved by the overlapping and interleaving of sclerites, pressure of spinelets, interlocking of setae, and the voluntary seizing of structures by organs modified for this purpose. Simultaneously, certain structures come in contact in a manner that suggests a stimulating function. Most of the following observations were made on a series of mounted specimens of *Ceratophyllus idius* Jordan & Rothschild, a common Nearctic bird flea that is principally found in the nests of purple martin, *Progne subis* (Linn.), and tree swallow, *Iridoprocne bicolor* (Vieillot).

The posterior few terga of the male are contracted (telescoped), this having the effect of elevating the valves of tergum VIII so that they embrace the posterior part of the female abdomen ventrally (fig. 7), the male sensilium being depressed and telescoped under tergum VII, the long antepygidial bristles of which extend dorsally, on either side of the venter of the female. The dense patch of spinelets on the dorsal inner surface of the male tergum VIII lie against the female sternum VII, and it seems probable that they assist in holding the tergum in position.

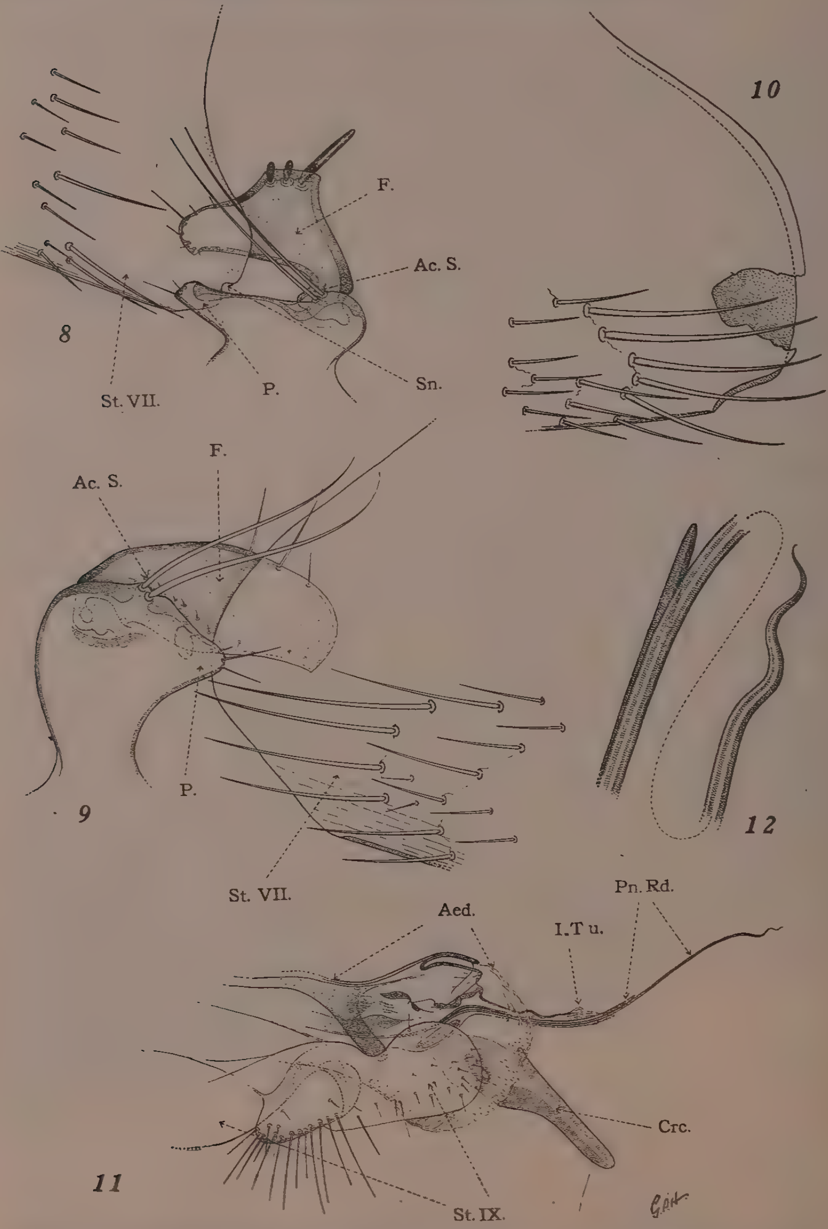
The movable process of each clasper is then inserted *under* the margin of the female sternum VII, in the vicinity of the sinus if there is one. The fixed process remains *outside* the margin of the sclerite (figs. 8 and 9). By muscular action the movable process is now closed so that the margin of sternum VII on either side is firmly " pinched " between it and the fixed process. The " lock " of the claspers (tubercle on the movable process ; groove on the fixed process), which is very well developed in some species, permits a very firm grip on sternum VII, and the writer has seen females of many species in which the margin of sternum VII has been broken and torn (fig. 10), presumably through mating activities.

As mentioned, the shape and armature of the clasper processes are of great taxonomic significance, there being a great variety of shapes, some of them appearing to be needlessly complicated. The setae of the movable process, which are frequently modified into heavy spiniforms, are inserted on the mesal surface of the margin ; therefore it appears that they are not utilised to exert pressure or traction on sternum VII of the female, but may bear on the underlying plate (T. VIII). The shape of the distal margin of sternum VII of the female is almost equally distinctive for species, so that to some extent the processes of the male and the sternum VII of the female may operate as a " lock and key ".

The rod-like sternum VIII of the male arches over the tip of the female abdomen so that its apical membranous flap is distributed over the proctiger and anal stylets of the female, while its long apical setae lie over the sensilium (fig. 13). In the living insects it was noted that the male frequently elevated and lowered sternum VIII so that its apical setae and membrane moved up and down over the female. In doing this the setae constantly " stroked " the long hairs arising from the trichobothriae of the sensilium, which may have transferred some stimulus. It would be dangerous to infer that this observation indicates the true function of the sensilium, as there was no clear indication as to how that organ in the male was stimulated (unless by some ventral setae of sternum VII of the female), and in any case the males of many fleas, including some ceratophyllids, do not have sternum VIII, or any alternative structure, sufficiently developed to reach the female sensilium during copulation.

Waterston (1912 : 78) also noted this activity of sternum VIII, and pointed out that the " stylets " were held in the U-shaped collar formed by the apical membranous flap of the " 8th tergite " (*sic* ! lapsus for sternite) ; he suggested that this pressure may serve to close the anus of the female, correlated as it appears to be with pressure directed from below through contact of the ventral, bristled lobe of sternum IX of the male against the anal sternum of the female (fig. 13).

(3) *Exposure of the genital aperture of the female.*—The terminalia now being firmly locked, a structural unit (figs. 11 and 13) composed of the aedeagus with its crochets, flanked on either side by the terminal lobes of sternum IX, is protracted a short distance to dilate the genital chamber of the female. It appears that the terminal lobes of sternum IX press laterally against the inner



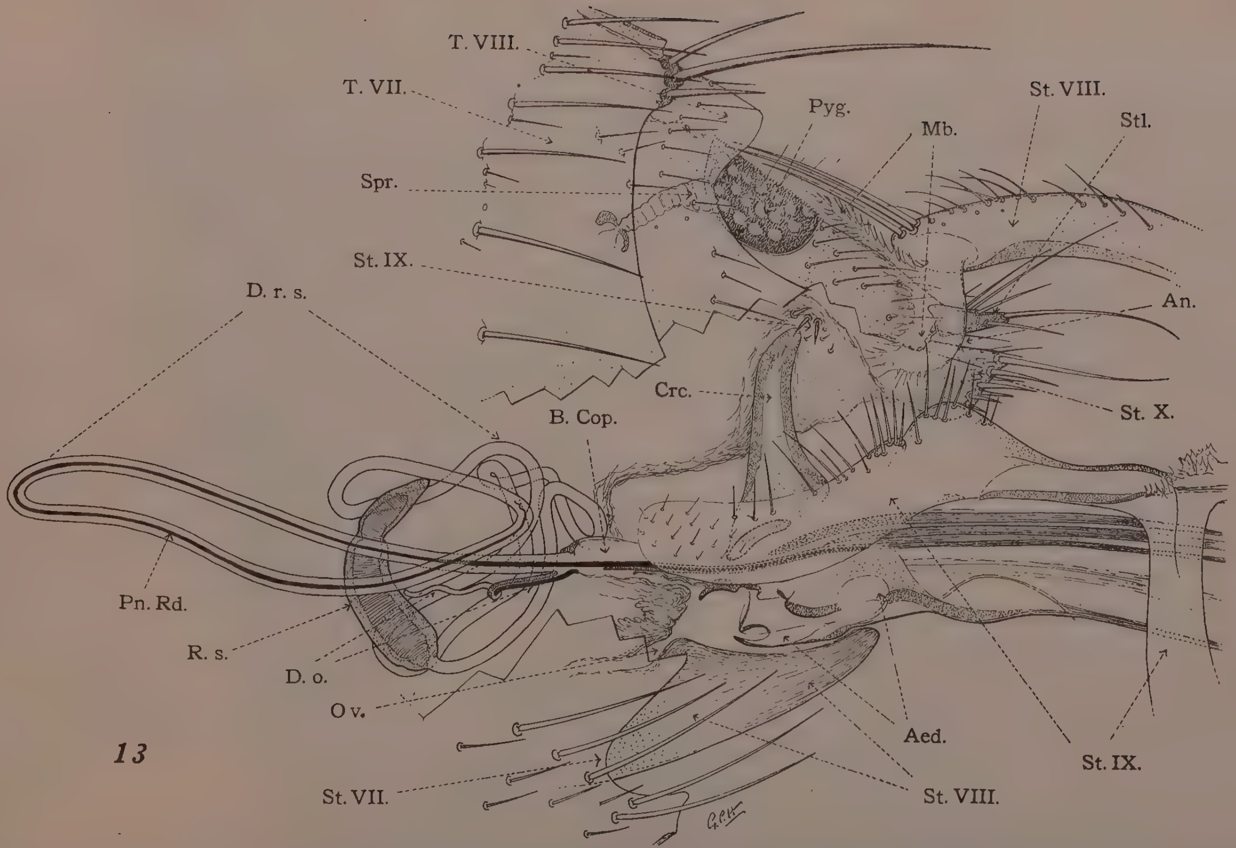
FIGS. 8–12.—(8) *Monopsyllus w. wagneri* (Baker) ; processes of male clasping sternum VII of female. (9) *Ceratophyllus rossittensis swansoni* Liu ; processes of male clasping sternum VII of female. (10) *C. lunatus tundrensis* Holland ; sternum VII of female, showing area on one side that has been torn away, presumably by male clasper. (11) *C. scopulorum* Holland ; apex of sternum IX and aedeagus of male, showing inner tube and protracted penis rods. (12) *C. idius* ; detail of penis rods. *Aed.*, aedeagus ; *Ac.S.*, acetabular setae ; *Crc.*, crochet ; *F.*, movable process of clasper ; *I.Tu.*, inner tube of aedeagus ; *P.*, fixed process of clasper ; *Pr.Rd.*, penis rods ; *St.* sternum.

surfaces of the female tergum VIII; while this position is being adopted the stout mesal setae of tergum VIII may serve as guides, ultimately engaging and interlocking with some of the setae near the mid point of the ventral margin of sternum IX.

The dorsal lobe of the aedeagus exerts pressure on the female sternum VIII, depressing it, while simultaneously the crochets engage with the setae on the membranous sternum IX, elevating it (fig. 13). The duct leading to the bursa copulatrix is exposed as a result of these operations, and the inner tube of the aedeagus aligned with it.

(4) *Insertion of the penis rods.*—The penis rods, which are the conveyors of the sperm, are now able to enter the bursa copulatrix. There are two rods, which apparently slide freely on each other, and (in *Ceratophyllus*) one appears to be longer than the other, or at least able to penetrate to a greater depth. Furthermore, their apices differ structurally (fig. 12). According to Snodgrass' (1946 : 70) description of a preparation of *C. r. swansoni*, one rod appeared to stop at the entrance of the " common spermathecal duct " whereas " the other is thrust through the bursal wall and extends far into the body cavity of the female ". It was suggested that this remarkable situation could be explained by a sudden muscular contraction in the dying flea with the result that the rod penetrated the haemocoele. However, a re-examination of Snodgrass' specimen and a study of other and better-prepared material, reveals the simple explanation that the deeply penetrating rod is encased throughout its length in a portion of the exceedingly long spermathecal duct, which it straightens out in the process! Of sixteen preparations of *C. idius*, four had the penis rods completely retracted; nine had one rod well inserted, but only three had both rods clearly visible. Fig. 13 illustrates the most extreme penetration observed. In no case did the second rod extend beyond the aperture of the blind duct, and it is tempting to speculate that this shortened rod is the non-functioning vestige of the sperm conveyor to an ancestral second spermatheca. The second rod was clearly visible in only four instances among the twenty-three pairs examined. It was smoothly rounded apically, whereas the first rod terminated in an undulating, whip-like tip (figs. 11, 12 and 13). Unfortunately, it has not been possible yet to ascertain the actions, or compare the structure of the penis rods, in species having two functional spermathecae; however, a figure published by Snodgrass (1946, pl. 19, L) suggests that in *Hystrichopsylla dippiei* Rothschild, at least, the apices of the rods are *not* similar.

Snodgrass (1946 : 70) wondered about the fate of the long outer part of the aedeagal inner tube, indicating that in his specimen of *C. r. swansoni* the penis rods had apparently penetrated its wall so that the tube itself was cast aside. In the writer's specimens, the tube was sometimes hard to detect, being delicate and membranous. However, in several specimens of *C. scopulorum* Holland it could be seen clearly, ensheathing the bases of the protracted penis rods (fig. 11). In a copulating pair of *C. niger* the rods were not protracted, but the tube could be seen, inserted well within the bursa copulatrix. In other specimens the tube was not always discernible. Its rôle in such species as *Amphalius necopinus* (Jordan), where the structure is extremely long and setaceous, is difficult to visualise. The female of this species has an extremely long and thick bursa copulatrix and it is possible that the inner tube as well as the penis rods are inserted deep into this organ, although how this is accom-


T. VIII.
T. VII.
Spr.
St. IX.
D. r. s.
Pyg.
Mb.
St. VIII.
Stl.
An.
St. X.
Crc.
B. Cop.
Pn. Rd.
R. s.
D. o.
O v.
Aed.
St. IX.
St. VII.
St. VIII.
G.P.H.

13

FIG. 13.—*C. idius.* Relations of male and female genitalia during copulation, showing the most extreme penetration of the penis rod observed in the series. *Aed.*, aedeagus ; *An.*, anus ; *B. Cop.*, bursa copulatrix ; *Crc.*, crochet ; *D.o.*, ductus obturatus ; *D.r.s.*, duct of spermatheca ; *Mb.*, membranous appendage of sternum VIII ; *Ov.*, oviduct ; *Pn.Rd.*, penis rod ; *Pyg.*, sensilium ; *R.s.*, spermatheca ; *Spr.*, spiracle ; *St.*, sternum ;

plished leaves one wondering. In the common squirrel flea, *Monopsyllus vison* (Baker), the inner tube is conspicuous, well sclerotised, and retracted in a sharp curve, but no doubt it can be extended during copulation.

Some fleas, e.g. the species of *Ceratophyllus* under discussion, have very long penis rods which, in the retracted state, are coiled up like a spring, along with the skeletal supports of the endophallus. Such species also have extremely long ducts leading from the bursa copulatrix to the spermatheca. It is interesting to note a strong correlation here, for it was observed that other species (e.g. *Ceratophyllus garei* Rothschild) which have short rods that are non-coiling have correspondingly short ducts.

It seems probable that the sperm-bearing rod is protracted and retracted rhythmically during copulation, although no original observations were made on this point. Mitzmain (1910 : 68) wrote of the " watchspring-like action of the spiral which, coiling and uncoiling, intermittently extends and withdraws the terminal apparatus ". Also, he noted the ". . . spermatheca . . . faintly discernible . . . as it swells and collapses ".

(5) *Completion of coitus and separation of the individuals.*—Mitzmain (1910) indicated that in *D. montanus* copulation occupied from two to four and a half hours. Waterston (1912) indicated from half an hour to an hour and a half with *C. farreni*, depending on temperature. Poole and Underhill (1953) mentioned two hours and " varying periods " with *M. clantoni*.

Mitzmain (1910 : 69) reported that, coitus being complete, the male initiates the release. He states ". . . the male attempted to free itself by pressing vigorously the mid and hind tarsi against the hind tibia of its mate. Simultaneously, the antennae were torn from the recumbent spines of the abdominal segments of the female. The abdomen was straightened, relaxing the clutch of the claspers ; the spiral contracted releasing the intromittent organ, and a final kick of the hind legs gave the male its liberty ". He stated, too, that males of *D. montanus* die soon after mating, dying even before the females lay their first batches of eggs.

Acknowledgments.

The writer gratefully acknowledges the loan of specimens of two pairs, *in cop.*, of *C. farreni* by F. G. A. M. Smit, Curator of the Rothschild Collection of Fleas, The Zoological Museum, Tring, Herts. ; of two pairs of *D. montanus* by Lt.-Col. Robert Traub, Chief, Department of Entomology, Army Medical Service Graduate School, Washington, D.C.; and of one pair of *C. r. swansoni* (the specimen studied by Snodgrass, 1946), by Dr. W. L. Jellison, Parasitologist, U.S. Public Health Service, Rocky Mountain Laboratory, Hamilton, Montana. Thanks are due, also, to J. E. H. Martin of the Systematic Entomology Unit, Ottawa, for assistance in collecting and preparing copulating specimens of *C. idius*, *C. niger*, and *C. riparius*.

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THE GENUS *CRATYNIUS* JORDAN (SIPHONAPTERA) AND ITS SYSTEMATIC POSITION, WITH A DESCRIPTION OF A NEW SPECIES.

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With 17 Text-figures.

Introduction.

In connection with studies on potential vectors and reservoirs of diseases, such as scrub typhus and leptospirosis, three joint U.S. Army-British Colonial Office Medical Research Units operated in North Borneo for two-month periods annually between 1951 and 1953. During these field projects extensive collections were made of fleas, chiggers, laelaptid mites and ticks of indigenous mammals. As a result it has become possible to discuss the systematics of the exceptionally rare genus *Cratynius* Jordan, 1933, a genus comprising fleas which seem to be characteristic parasites of the seldom-collected lesser gymnuran, *Hylomys suillus*, an insectivore related to the hedgehogs. In the present paper the value of certain characters heretofore much used in classification of fleas on the family or subfamily level is discussed. The affinities of *Cratynius* are also considered, the genus is redescribed, and a new species is described and figured. It seems to us particularly appropriate that a collection obtained by United States-British Research Units should be dealt with in a paper which is also the result of British-United States collaboration and that a paper on a subject so near to Dr. Jordan's heart as the higher classification of the Siphonaptera should appear in a volume published in his honour.

A. The "Families" Amphipsyllidae and Leptopsyllidae.

Two of the most conspicuous distinctions between different groups of fleas are the presence or absence of a genal comb and the degree of development of the interantennal suture,[1] which may be so strongly developed that the dorsal outline of the head is broken and the frons overlaps the occiput (when the flea is stated to be fracticipit) or may be vestigial or absent (integricipit). It is, therefore, hardly surprising that these characters were used from a relatively early date to make major divisions of the fleas, though it is now generally accepted that neither character is of more than minimal phylogenetic significance, nor is it to be wondered at that traces of the use of these characters still persist in the arrangement of the genera of fleas shown in Table I, and which are currently usually referred to the families Amphipsyllidae and Leptopsyllidae.

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[1] The terminology employed in this paper is that of Hopkins and Rothschild (1953) except for the phallosome, for which we use the terminology of Traub (1950*a*).

TABLE I.—*A list of the genera of fleas commonly referred to the families Amphipsyllidae and Leptopsyllidae, with note of the presence or absence of a genal comb and of whether the head is fracticipit or integricipit in the female. An interantennal suture may be well developed in genera which must be considered integricipit and it is sometimes difficult to tell in the male sex whether the head is fracticipit or not.*

Name.	Genal comb present.	Head fracticipit or integricipit.
LEPTOPSYLLIDAE.		
Acropsylla	Yes	I
Cratynius (= *Johnsonaepsylla*)	No	F (♂), I (♀)
Leptopsylla	Yes	F
Paractenopsyllus	Yes	F
Pectinoctenus	Yes	F
Peromyscopsylla	Yes	F
Sigmactenus	Yes	F
AMPHIPSYLLIDAE.		
Amphipsylla	No	I
Brachyctenonotus	No	I
Caenopsylla	Yes	I
Ctenophyllus	No	I
Cystipsylla	No	?
Desertopsylla	Yes	?
Dolichopsyllus	No	I
Frontopsylla	No	I
Geusibia	No	I
Mesopsylla	Yes	I
Odontopsyllus	No	I
Ophthalmopsylla	No	I
Paradoxopsyllus	No	I
Phaenopsylla	No	I

The earliest supra-generic division of the fleas was by Taschenberg (1880), who recognised only Pulicidae and Sarcopsyllidae (now called Tungidae), but the earliest formal attempt to subdivide the Pulicidae (in Taschenberg's sense) into subfamilies (Tiraboschi, 1904: 243, 275, 296) was based at least mainly on the presence or absence of a genal comb. As a result, the members of the groups under discussion which possess a comb were placed widely apart from those in which it is absent. Oudemans (1908 : 92, and 1909 : 133–158) attached enormous importance to the degree of development of the interantennal suture and based on it his division of the fleas into two supposed suborders which he called Integricipita and Fracticipita. Since all the genera of the group under discussion which were known at that time were either fracticipit and had a genal comb or were integricipit and had no genal comb, this arrangement appeared to fit them very well, and the separation of the two groups was made even wider than before. In the main, Oudemans' classification has held the field, at least so far as the groups under consideration are concerned, almost until now. Ewing (1929 : 159), for instance, used the head-character in the second couplet of his key while Wagner (1939), though recognising to some extent (p. 62) the great variability of the head-character and abandoning Oudemans' supposed suborders, still divided the families mainly in conformity with this character. The classification of Ewing and Fox (1943) was almost the same as that of Ewing (1929).

In recent years, however, a number of specialists have come to the conclusion, apparently largely independent of one another, that the degree of development of the interantennal suture is not a character of much phylogenetic importance and that the groups typified by *Leptopsylla* and *Amphipsylla* are more closely related than was hitherto supposed. Jordan (*in* Smart, 1948) recognised (pp. 227, 244) a family Amphipsyllidae (with subfamilies Amphipsyllinae, Mesopsyllinae and Dolichopsyllinae) and placed the Leptopsyllidae next to them, though without making an explicit statement that he considered the two groups closely related. His views on the value of the interantennal suture for primary divisions are, however, easily to be deduced from his treatment of the Hypsophthalmidae (pp. 223, 225, under the name Chimaeropsyllidae), in which he included both fracticipit genera as well as others in which there is no trace of an interantennal suture. Holland (1949) placed the Amphipsyllinae (p. 108), the Dolichopsyllinae (p. 111) and the Leptopsyllinae (p. 173) as subfamilies of Ceratophyllidae. He noted important characters in which the Leptopsyllinae are ceratophyllid rather than hystrichopsyllid, but evidently did not consider the Leptopsyllinae to be specially closely related to the other two groups, since he placed the Ceratophyllinae between them. Ioff (1949) remarked on the over-importance which has been attached to the structure of the head capsule. He treated Paradoxopsyllinae (p. 49), Mesopsyllinae (p. 73) and Leptopsyllinae (p. 74) as separate subfamilies of Ceratophyllidae, and made a notable change by including the combless genus *Amphipsylla* under Leptopsyllidae. However, he gave no definitions of the subfamilies, nor a key to them, and hence the significance of his arrangement is not easy to evaluate, more especially since the next three groups (also treated as subfamilies of Ceratophyllidae) all belong in reality to the Hystrichopsyllidae. Traub (1950*a* : 93, 105) noted that the structure of the phallosome in *Leptopsylla* confirmed its ceratophyllid rather than hystrichopsyllid affinities. A little later (1950*b* : 136) he placed in Leptopsyllinae a genus (*Acropsylla*) hitherto considered to be amphipsylline. Hopkins and Rothschild (1953 : 3–6) published a list of the genera of fleas with the families and subfamilies to which Dr. Jordan assigned them, in which the families Amphipsyllidae and Leptopsyllidae were recognised. They made no attempt at that time to evaluate the characters separating these two groups, and at a later date Dr. Jordan informed them that he thought the two groups were closely related and might well be reduced to the rank of subfamilies.

The discovery by Traub of the genus which he described (1952) as *Johnsonaepsylla* made an investigation of the question urgent. In that paper, both Amphipsyllinae and Leptopsyllinae were recognised as subfamilies of Ceratophyllidae, and the way in which *Johnsonaepsylla* links them was pointed out. Differences between Ceratophyllidae and Hystrichopsyllidae were also discussed. Independent studies of specimens of *Johnsonaepsylla* by each of the present authors led to re-examination of the criteria hitherto used to separate the two groups typified by *Amphipsylla* and *Leptopsylla* and to their deciding that if Leptopsyllidae and Amphipsyllidae can be separated at all, it must be at no higher rank than subfamilies and on some other character than the degree of development of the interantennal suture. On the basis of the study of Borneo specimens, including the new species herein described, it was also decided that *Johnsonaepsylla* (known only in the male sex, which is fracticipit) is a synonym of *Cratynius* Jordan, 1933 (known only from the female, which is integricipit). A further character which had been suggested as separating genera allied to *Leptopsylla* from those more closely related to *Amphipsylla* also proved useless, for among genera obviously belonging in the latter category, some have 5 lateral pairs of bristles on the margins of the fifth segment of the hind tarsus, as in *Leptopsylla*, some have the members of the first pair approximated to one another by being shifted mesad to a greater or lesser degree, while in yet others this displacement has proceeded so far that these bristles lie between the members of the second pair.

The family which contains the groups typified by both *Amphipsylla* and *Leptopsylla* appears to be very near Ceratophyllidae, though the possibility that some of the resemblances may be due to parallelism cannot be excluded. It agrees with Ceratophyllidae (and differs from Hystrichopsyllidae) in the following characters: (1) Metanotum with apical spinelets; sensilium with almost straight dorsal margin. (2) Male with an apodemal rod arising as a tendon from the ninth sternite. (3) Proportions of dorsal and ventral sclerites of eighth segment very variable, but eighth tergum usually much larger, and eighth sternum often much smaller, than in Hystrichopsyllidae. (4) Crochets typically large, articulated and movable (relatively small and not freely movable in Hystrichopsyllidae). It is separable from Ceratophyllidae as follows: (1) Uppermost bristle of ocular row at or near the margin of the antennal fossa and above the level of the upper margin of the eye (in front of the eye in Ceratophyllidae). (2) An arch of the tentorium (fig. 1, *T.A.*) always visible in front of the eye unless concealed by a very extensive genal comb (genal comb always absent in Ceratophyllidae and arch of tentorium absent from this position).[2] (3) Sternite VIII of male never more than moderately reduced. (St. VIII greatly reduced in Ceratophyllidae.) (4) Wagner's gland always absent. (Wagner's gland nearly always present in Ceratophyllidae.)

Turning to the name to be used for the family thus defined, we first note that, whereas hitherto there has been no such thing as priority for family names in zoology, the Fourteenth International Congress of Zoology accepted (*Copenhagen Decisions on Zoological Nomenclature*, para. 45) the principle of priority for "Family-Group names" (defined as names for all categories between the Generic Group and the Ordinal Group) and decided (para. 46) that all such names should be co-ordinate with one another, i.e., that a name first given to a tribe or subfamily should retain its original seniority even if the group concerned should later be considered to be a family or subfamily. A further provision which concerns us is that (para. 54b) by which the name of a taxon in the family category is to be changed if it is found to be based on a generic name which is a junior homonym. It is clearly implied that the replacing name inherits the seniority of that which it replaces. In both the paragraphs there is provision for the maintenance of current usage in instances in which strict application of priority would not be conducive to "stability and universality of nomenclature". Since all names in the family category are co-ordinate, the names in this category which have as their type genera taxa belonging to the group under discussion are, in order of seniority and with their original terminations, as follows: Leptopsyllidae Rothschild, 1915 (replacement for Ctenopsyllidae Baker, 1905, which is invalid because based on a junior homonyn, and taking the seniority of Ctenopsyllidae); Dolichopsyllinae Baker, 1905; Amphipsyllina Ioff, 1936; Paradoxopsyllini Ioff, 1936; Brachyctenonotini Ioff, 1936; Mesopsyllinae Wagner, 1939; and Odontopsyllini Wagner, 1939. Thus, Leptopsyllidae and Dolichopsyllidae have ten years' priority over any other names which might be applied to the family, and the former has page-precedence, since Ctenopsyllidae was first mentioned by Baker on page 124, whereas Dolichopsyllinae appeared first on page 127. The " first reviser " principle does not enter into the matter, since (so far as we are aware) no author has made a deliberate choice between these two names, which have not been considered to be synonymous.

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[2] Thread-like vestiges of it are present in some species.

Leptopsyllidae is also probably the name which has been most used for any portion of the family. The name Ctenopsyllidae has been used by a few German and Russian authors who chose to ignore the fact that *Ctenopsyllus* Kolenati, 1863, is a junior homonym of *Ctenopsyllus* Kolenati 1857, of which it is not a synonym. The principle protagonist of this view died in 1944 and the foremost Russian siphonapterologist recently announced (Ioff, 1949: 74) his abandonment of the name Ctenopsyllinae in favour of Leptopsyllinae, which thus became the name almost universally used for this portion of the family. This so-recent achievement of almost complete uniformity after half a century of controversy would be a most cogent argument for the retention of the name Leptopsyllidae in its current sense even if it were not the senior name. The next to it in seniority is Dolichopsyllidae, but this is open to very strong objections because of the way in which it was abused by Ewing (1929: 159, 166–172), who (by using criteria of minimal phylogenetic importance) succeeded in including under the name no less than eight separate families, or portions of them. Ewing's concept of the Dolichopsyllidae has achieved far wider currency than would otherwise have been the case by its inclusion in slightly modified form in the classification of North American fleas by Ewing and Fox (1943) and in the list of the fleas of the world published by Costa Lima and Hathaway, but its use has been confined to America and even there has been rejected by all the leading siphonapterologists. The use of the name Leptopsyllidae for the family is, therefore, in accordance with current practice as well as with the Copenhagen Decisions, and this also applies to the use of Leptopsyllinae for the subfamily typified by *Leptopsylla*.

The case of the other subfamily is more difficult, because, though there is no doubt that under the Copenhagen Decisions its name should be Dolichopsyllinae, the objections to this name are so strong that we think it should not be employed. *Dolichopsyllus* is an aberrant genus constituting a tribe by itself and is therefore highly unsuitable as the type genus of any taxon larger than this tribe. The only authors who do employ it for any larger taxon are those who follow Ewing in misapplying it to a heterogeneous collection of genera belonging to a number of unrelated families. All the foremost workers on fleas are strongly opposed to its use for a subfamily, whereas the name Amphipsyllidae (or Amphipsyllinae) is in use by almost every author who recognises the taxon. Since in any case the Copenhagen Decisions will necessitate an appeal to the International Commission on Zoological Nomenclature to preserve some of the best-known names of families of Siphonaptera (Tungidae, Malacopsyllidae, Pygiopsyllidae and Ischnopsyllidae) to say nothing of the name of the order itself, we think that the name Amphipsyllinae should be included in this appeal and meanwhile intend to use this name for the taxon typified by *Amphipsylla*.

B. THE GENUS *CRATYNIUS*.

Before discussing the separation of the two subfamilies it is desirable to discuss and redefine the genus *Cratynius* (especially now that males and females have been associated for the first time), and it is also advisable first to describe both a new species from North Borneo and the heretofore unknown female of *C. audyi*. Most of the characters cited in the redescription of the genus are from Traub (1952) and Jordan (1933).

Cratynius Jordan, 1933.

Cratynius Jordan, 1933, *Novit. zool.* **38** : 352. (Female only.)
Johnsonaepsylla Traub, 1952, *J. Wash. Acad. Sci.* **42** (9) : 289. (Male only.) **Syn. n.**

Fracticipit or virtually so in male ; integricipit in female. Eye reduced, but distinct. Frons (preantennal region) with three rows of bristles ; some of first row somewhat spiniform. Frontal tubercle distinct. Occiput (postantennal region) with three rows of bristles. Antennal segment II with bristles short, not reaching beyond proximal fifth of club in either sex. Antennal fossa not extending on to propleuron. Labial palp much shorter than fore coxa. First link-plate received in distinct sinus of prosternosome. Fore femur with very few lateral and mesal bristles. Some of dorsolateral bristles of fore tibia short and straight, forming a reduced false comb. Mesonotum with subdorsal marginal pseudosetae or spinelets. Meso- and metanota dorsally heavily incrassate. Pronotal comb consisting of more than 18 narrow spines which are longer than pronotum. Pronotum with one row of long bristles. All tibiae with three long dorsal bristles (subbasal, median and apical)—the other bristles short. Sterno-episternal ridge of mesothorax sclerotised throughout and very conspicuous. Metepisternum ("lateral metanotal area") distinct. Pleural arch well-developed. Mid and hind coxae lacking both mesal spiniforms and a row of mesal marginal thin bristles. Metanotum with apical spinelets. Tibial false comb vestigial on mid and hind legs. Some of typical abdominal terga with apical spinelets. Unmodified terga usually with two rows of bristles, but first row reduced or absent on some. Margins of sclerites at times minutely denticulate. Basal abdominal sternum with about one pair of ventromarginal bristles. Spiracles subovate. Male with three antepygidial bristles ; female with three to five. Male eighth tergum fairly well developed, extending as far caudad as near middle of clasper. Male eighth sternum relatively large and unmodified, broader than long. Movable process of clasper lacking spiniforms. True acetabular bristles absent. Apical appendage of aedeagus long. Sclerotised inner tube oblique and relatively unarmed. Crochets very large, conspicuous. Distal arm of ninth sternum narrow, sinuate, devoid of spiniforms. Female eighth sternum fairly large but weakly sclerotised. Anal stylet more than twice as long as broad at base. Spermatheca with tail about twice as long as head, but tail may be either very stout (more than diameter of head) or relatively narrow (i.e., distinctly narrower than head). Duct of spermatheca well sclerotised, long, vermiform, coiled.

Cratynius crypticus sp. n. (figs. 1–9 and 11).

Immediately separable from *C. audyi* (Traub, 1952) in that the basal arm of the male ninth sternum (fig. 9, *B.A.*9) bears two long bristles arising from a median hump (a most unusual occurrence in fleas) and in that the apical arm of the ninth sternum (*A.A.*9) lacks a distinct ventromedian lobe. Apex of crochet evenly ovate (fig. 3); not recurved upward like the head of a hammer. Female distinguishable from both *C. audyi* and *C. bartelsi* Jordan, 1933, by the peculiar spermatheca (fig. 7) in which the tail is very stout, apically even broader than the head, and is scarcely differentiated from the head, instead of being long and narrow (fig. 14). Frontal tubercle placed higher than in *C. audyi*—in the male it is situated well above the midpoint (fig. 1, *TB.*) instead of at that level, while in the female the tubercle (fig. 11, *TB.*) is at the level of the midpoint instead of clearly below it (fig. 12, *TB.*). With the sterno-episternal ridge of mesothorax (fig. 8, *SE.R.*) extremely well developed, even much more so than in *C. audyi* (fig. 13, *SE.R.*). Dorsal incrassation of terga also relatively more pronounced than in *C. audyi*. Lacking a squamulum on metepisternum (fig. 8, *MTST.*), whereas *C. audyi* has a well-developed squamulum (fig. 13, *SQ.*).

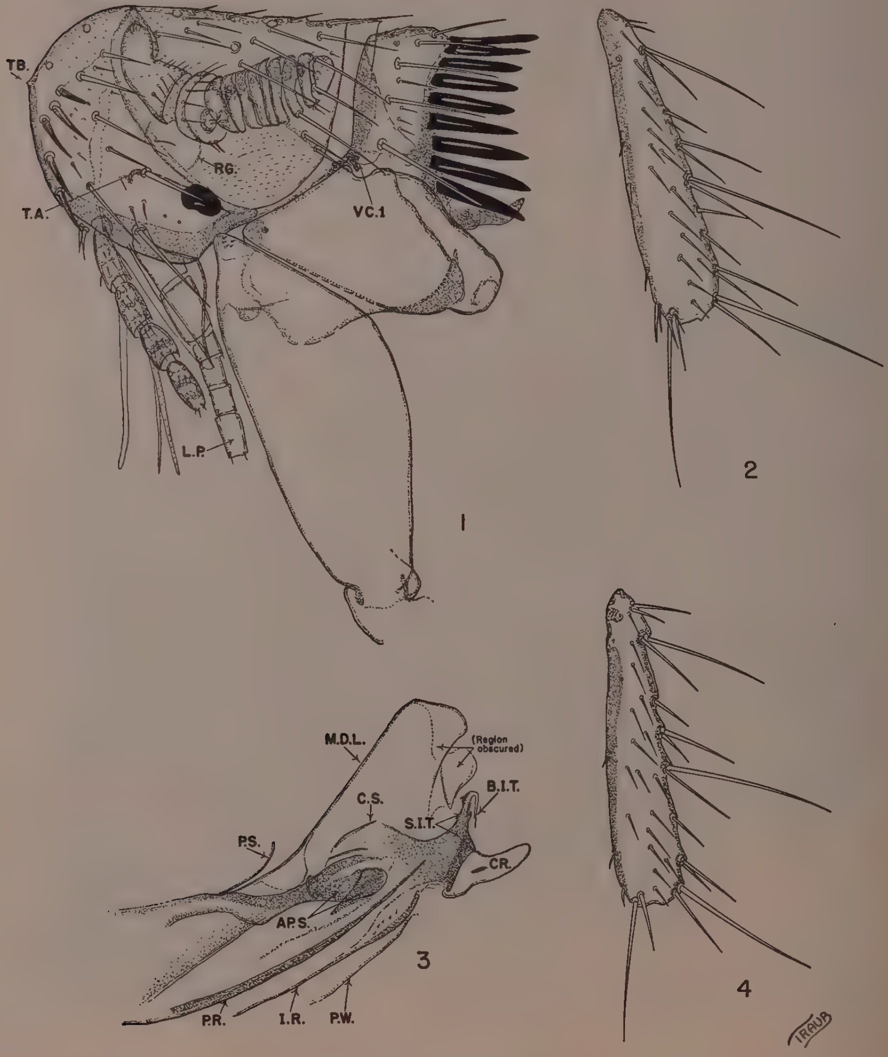
Head, male (fig. 1).—Frons with bristles as follows: first row of seven, lower five of which are stout and more or less spiniform. Uppermost spiniform at level of frontal tubercle (*TB.*) in male; in female above this level (fig. 11). In male second row of three large bristles, of which uppermost is almost at level of frontal tubercle; middle bristle displaced caudad, well out of line; in female this row with only two bristles, uppermost somewhat below level of frontal tubercle. Third row of two long bristles, uppermost at or somewhat above level of eye. Eye small, only about two and one-half times diameter of adjacent incrassation of antennal fossa. Genal process subacute. Anterior wing of maxillary lobe indistinct, very weakly sclerotised. Labial palp (*L.P.*) five-segmented, extending only about half length of fore coxa. Second antennal segment with apical bristles short, not reaching beyond apex of second segment of club in male, and third in female. Occiput with bristles arranged: 5 (sometimes one out of line)–4 (or 5)–6 (or 7) each side. Ventralmost of last row displaced to ventrocaudal angle.

Thorax.—Pronotum with a row of about five or six bristles per side; small intercalaries somewhat displaced caudad. Comb with a total of about 19–21 spines, the spines long and narrow, ventralmost slightly broader than pronotum proper. Mesonotum (fig. 8, *MSN.*) heavily incrassate subdorsally, as are all thoracic terga; with three rows of bristles. Mesonotal collar with one or two subdorsal apical spinelets or pseudosetae each side, representing heavily sclerotised versions of the pseudosetae of *C. audyi*. Mesepisternum (*MPS.*) and mesepimeron (*MPM.*) each with three or four bristles, the higher number due to the apparent position of a bristle near the dorsal margin of the pleural ridge. Sterno-episternal ridge of mesothorax unusually well developed. Mesosternum (*MST.*) well developed, broader than mesepisternum. Metanotum (*MTN.*) together with its collar, about as long as entire mesonotum; with three rows of bristles, but first row consisting of merely one or two bristles. Metanotal collar with one dorsoapical spinelet each side. Metepisternum (= "lateral metanotal area") (*MTS.*) about two-thirds as broad as long; with two bristles, uppermost placed further caudad and very long. Metasternum (*MTST.*) with one long bristle near the well developed pleural arch (*PL.A.*). Metepimeron (*MTM.*) usually with about six bristles, frequently arranged 2–3–1. Metathoracic spiracle ovate, slightly broader than long.

Legs.—Femora and tibiae essentially as in *C. audyi*, but legs in general relatively even longer and narrower than in that species, e.g., segment I of hind tarsus about eight times as long as broad, not six. None of tarsal bristles reaching beyond apex of following segment. Hind tibiae in both sexes with three of the dorsomarginal pairs of bristles each including an extremely long bristle; these pairs are: (1) subproximal; (2) just below middle; (3) apical. In the female (fig. 2) there are often two single marginal bristles below the middle pair; in the unique male there is only one such bristle on one leg (fig. 4) but two on the other. Measurements (in microns) of tibiae and segments of tarsi (petiolate base omitted) of holotype:

Leg.	Tibia.	Tarsal segments.				
		I.	II.	III.	IV.	V.
Fore . . .	111	94	80	75	55	106
Mid . . .	316	210	102	95	61	118
Hind . . .	492	400	180	120	70	122

Last tarsal segment on each leg with five lateral plantar bristles, the bristles relatively long and thin.

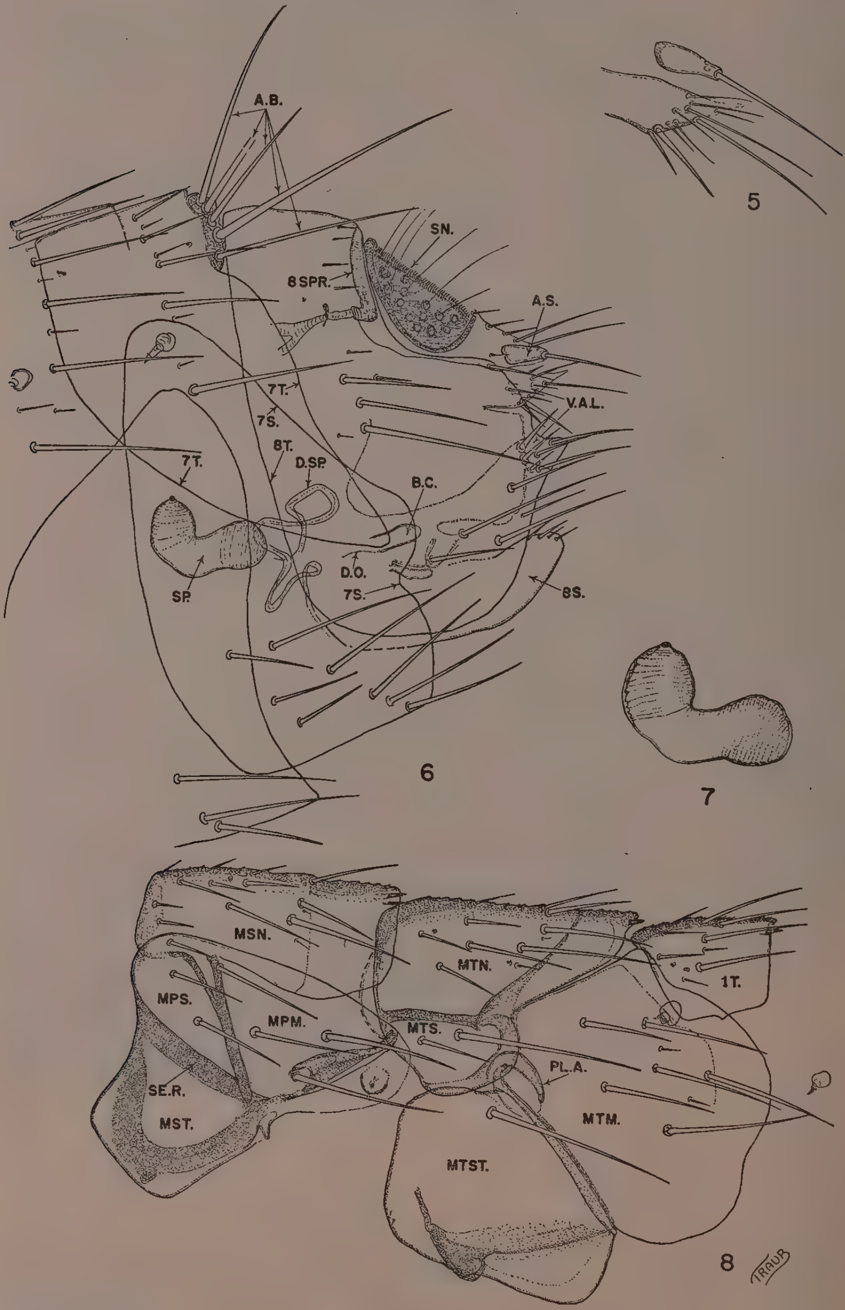

TB.
T.A.
RG.
VC.1
L.P.
1
2
M.D.L.
(Region obscured)
C.S.
B.I.T.
S.I.T.
P.S.
CR.
AP.S.
3
P.R.
I.R.
P.W.
4
TRAUB

Figs. 1–4.—*Cratynius crypticus* sp. n. (1) Head and prothorax, male. (2) Hind tibia, female. (3) Distal portion of phallosome. (4) Hind tibia, male.

Abdomen.—Terga subdorsally heavily incrassate. Dorsal margins appearing somewhat serrate; posterior margins minutely denticulate. First tergum with two rows of bristles and usually two subdorsal spinelets per side; basal sternum with one ventromarginal bristle per side in each sex. In the male, and usually in the female, terga II, III and IV with one dorso-apical spinelet per side. Typical terga in the male with first row of bristles represented by two or three bristles, but the numbers progressively decreasing until sixth tergum has merely one bristle per side in this row; in female first row usually with three or four bristles per side. Ventralmost bristle of second tergal row inserted below spiracle. Typical sterna in each sex with about three bristles per side. Three antepygidial bristles in male, of these middle one slightly longer than others; female with three to five antepygidial bristles (fig. 6, *A.B.*).

Modified abdominal segments (*male*, figs. 9 and 3).—Eighth tergum (*8T.*) extending as far caudad as proximal third of fixed process of clasper and just beyond aedeagus (phallosome); with two long subdorsal bristles and one submedian one; with one short thin bristle immediately above the two more anterior long bristles. Eighth sternum extending apicad only to a point slightly distad of an angle of the ninth sternum or of apical margin of eighth tergum; extending dorsad to about level of manubrium and therefore somewhat broader than long; with one subventral bristle. Fixed process of clasper (*P.*) long and subovate, resembling that of *C. audyi*; about five-eighths as broad as long. Dorsal margin slightly convex but actually straight for most of its length. Ventral margin flattened for most of its length, paralleling dorsal margin. Fixed process (*P.*) with two caudomarginal bristles inserted fairly near apex and a group of about five thin subdorsal bristles on apical fifth. Movable process or digitoid (*F.*) extending to dorsal margin of fixed process; apically subtruncate; anterior margin straight; caudal margin slightly convex, essentially subparallel with anterior margin; with a fairly long subapical caudomarginal bristle; dorsal margin with one or two thin bristles; with a few thin hairs scattered over surface and three small thin caudomarginal bristles near insertion of fixed process. Manubrium resembling that of *C. audyi*, fairly long and narrow, apically somewhat upturned. Ninth sternum with basal arm (*B.A.*9) subequal in length to apical arm (*A.A.*9); relatively long and narrow, apically subacuminate; resembling a slightly crooked finger. Morphological dorsal (apparently caudal) margin with a conspicuous hump near ventral third; this hump bearing one or two long bristles. Apical arm of ninth sternum (*A.A.*9) also relatively long and narrow; vermiform; about 13 times as long as broad at middle. Its ventral margin sinuate, not produced into any definite lobes, and with a low convexity near middle denoted by a long bristle at this point; above and below this a small bristle and another such small bristle at apical fourth. Apically, slightly expanded and somewhat upcurved; with a subapical group of about nine or ten thin bristles. Aedeagal apodeme (penis plate) with a long apical appendage and well developed proximal spur (fig. 3, *P.S.*) as in *C. audyi*. Median dorsal lobe (*M.D.L.*) quite straight. End-chamber partially obscured by processes of clasper in only known specimen, so that apicomedian sclerites cannot be seen. Crescent sclerite (*C.S.*) slightly convex. Crochets (*CR.*) quite long, shaped like a shoe. Sclerotised inner tube (*S.I.T.*) fairly short, about two and one half times as long as broad at maximum. With short but distinct band of inner tube (*B.I.T.*) extending from apex. Wall of aedeagal pouch (*P.W.*) lightly sclerotised. Penis rods long but not fully coiled, paralleling apodemal rod of ninth sternum (fig. 9, *AP.R.*9). Ventral intramural rod of endophallus (*I.R.*) well sclerotised.

Modified abdominal segments, female.—Seventh sternum (fig. 6, 7*S.*) with caudal margin bearing a shallow sinus, the resulting upper lobe broad, its margin somewhat convex; ventral (lower) lobe longer, subtruncate. Seventh sternum with an oblique row of about five long bristles per side, beginning near upper level of ventral lobe and extending to ventrocaudal angle; this row preceded by a group of about three smaller bristles. Eighth tergum (8*T.*) with anterior margin at about level of antepygidial bristles; with a group of three large submedian bristles below sensilium, virtually in line with long narrow spiracle; with three submedian long bristles at level of sinus of seventh sternum; caudal margin


A.B.
SN.
8 SPR.
A.S.
7T.
V.A.L.
7S.
8T.
D.SP.
B.C.
7T.
SP.
D.O.
7S.
8S.
5
6
7
MSN.
MTN.
1T.
MPS.
MPM.
MTS.
PL.A.
SE.R.
MST.
MTM.
MTST.
8
TRAUB

Figs. 5–8.—*Cratynius crypticus* sp. n. (5) Ventral anal lobe and anal stylet. (6) Modified abdominal segments, female. (7) Spermatheca. (8) Meso- and metathorax, male.

produced into a median, thumb-like projection below ventral anal lobe; with three or four submarginal fairly long thin bristles below this point and adjacent to a vertical group of three stout mesal bristles. Eighth sternum (*8S.*) weakly sclerotised but large; dorsal margin with an apical group of short thin bristles. Anal stylet (*A.S.* and fig. 5) about two and one-half times as long as broad at maximum, slightly bent ventrad, with a long apical bristle and one or two subapical dorsal hairs. Ventral anal lobe (*V.A.L.* and fig. 5) with ventral margin angulate and with a stout bristle at the angle; with a long subapical bristle; with about two or three thin hairs between the two conspicuous bristles and about two such thin bristles dorsad of the subapical one. Spermatheca (*SP.* and fig. 7) with tail short and broad, about twice as long as the head, which can only be distinguished by virtue of its annulae; tail with apical portion slightly dilated, somewhat resembling head in size and shape. Bursa copulatrix (*B.C.*) not well differentiated, with only lateral margins well chitinised; apically semimembranous; with a small blind duct (*D.O.*). Duct of spermatheca (*D.SP.*) well developed, long, vermiform, the sclerotised portion about twice as long as spermatheca.

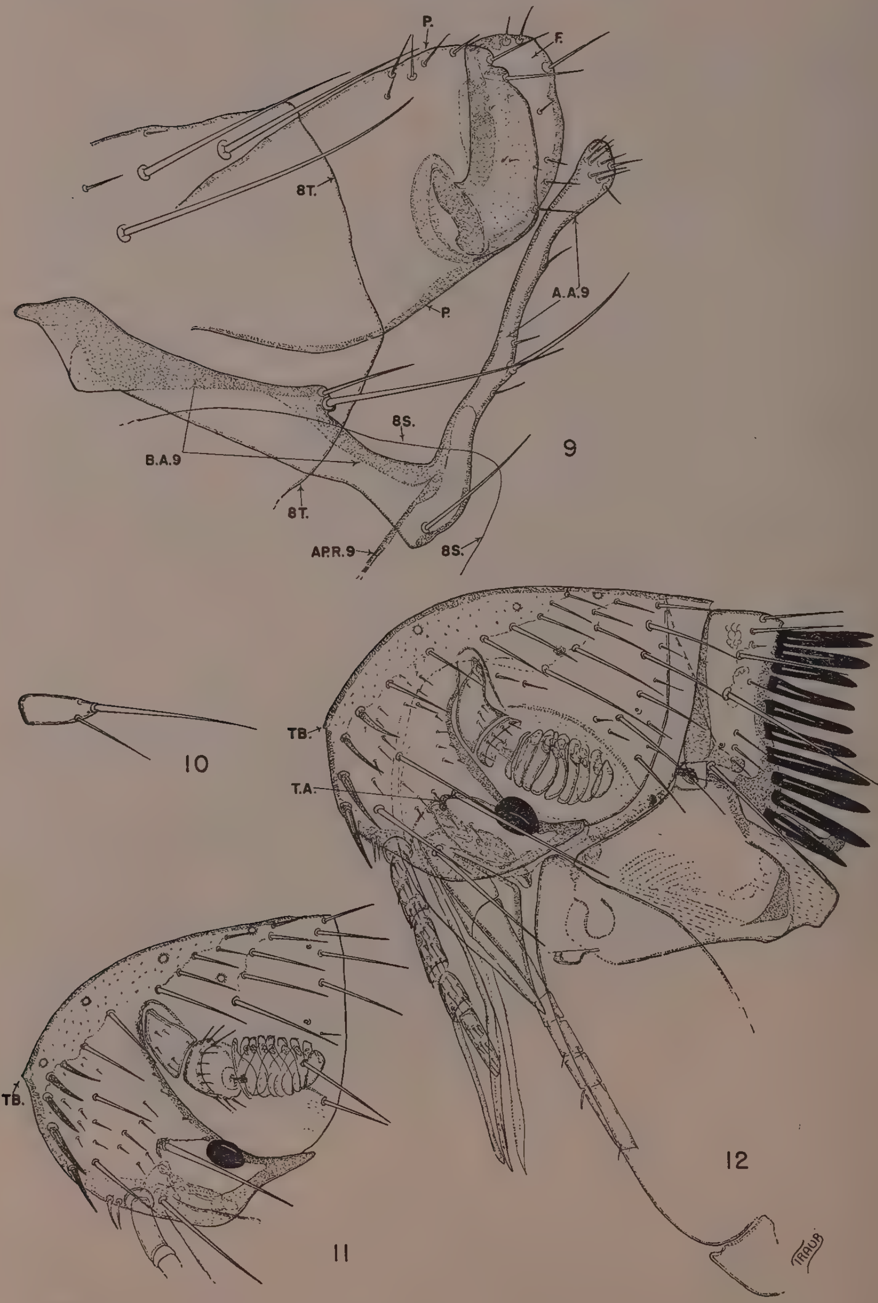
Type material.—Holotype male (R.T. No. B19202–1) *ex Hylomys suillus*, the lesser gymnuran, NORTH BORNEO: Mt. Kinabalu, Tenompak, elev. 4500 ft., 12.viii.1953 (*R. Traub*). Deposited in U.S. National Museum (U.S.N.M. No. 62478). Allotype female (R.T. No. B19310–1), *ibid.* but 20.viii. Three paratype females as follows: one with same data as holotype; a second with data of allotype; a third from *Rattus alticola*, *loc. cit.* but near Bundu Tuhan, elev. 4000 ft., 15.vi.1952 (*J. R. Audy*). One paratype in the collection of the British Museum (Nat. Hist.) at Tring; the remainder in R. Traub's collection.

Cratynius audyi (Traub, 1952).

Johnsonaepsylla audyi Traub, 1952, *J. Wash. Acad. Sci.* **42** (9): 289–296, figs. 1–8 (male only).

Female.—Near *C. bartelsi* Jordan, 1933, but separable by the characteristic shape of the seventh sternum (fig. 16, *7S.*), in which the upper margin of the deep narrow sinus is apically excised for half its length, and in which the ventral lobe is quite truncate. The upper lobe is very broad, much more so than the ventral lobe. In *C. bartelsi* the upper margin of the sinus is entire, not excised, and the lobe above the sinus is rounded and much narrower than the ventral lobe; the apical margin of the latter is oblique and nearly straight in its dorsal half and more or less rounded in its ventral half. The long, fairly narrow tail of the spermatheca (as in *C. bartelsi*) serves to separate this species from *C. crypticus* sp. n.

Head (fig. 12) resembling that of male except for secondary sexual characteristics of family, such as lower position of antennae and of frontal tubercle and greater breadth of frons; wholly integricipit. *Thorax* (fig. 13) essentially as in male. Posterior margins of abdominal terga minutely denticulate, as in male. Three antepygidial bristles per side. Seventh sternum (fig. 16, *7S.*) with caudal margin bearing a fairly deep narrow sinus; dorsal margin of sinus sinuate; upper lobe broad, its lower portion fairly straight. Lower (ventral) lobe shorter than upper, truncate. Seventh sternum with an oblique row of about five or six bristles, of which the lower three are much longer than the remainder, this row immediately preceded by a row of one to three much smaller bristles. Eighth tergum (*8T.*) somewhat resembling that of *C. crypticus* sp. n., but only one long bristle immediately below sensilium and with only two submedian bristles near level of sinus of seventh sternum. Anal stylet (*A.S.* and fig. 10) about two and one-half times as long as its maximum breadth; with a long apical bristle and a fairly long ventral one. Ventral anal lobe (fig. 17) with ventral margin sinuate, bearing two long bristles (one of these very stout) at ventrocaudal angle; with two long bristles near middle; with about four or five small thin submedian lateral bristles and two or three smaller marginal ones. Spermatheca (*SP.* and fig. 14) with


P.
F.
8T.
A.A.9
P.
B.A.9
8S.
8T.
AP.R.9
8S.
9
10
TB.
T.A.
TB.
11
12
TRAUB

FIGS. 9–12.—*Cratynius crypticus* sp. n.—(9) Processes of clasper and ninth sternum. (10) *C. audyi* (Traub): Anal stylet. (11) *C. crypticus*: Head, female. (12) *C. audyi* (Traub): Head and prothorax, female.

tail about twice as long as head and evenly vermiform, distinctly narrower than head and upturned near midpoint. Bursa copulatrix (*B.C*) scarcely broader than well-developed duct of spermatheca (*D.SP*) ; long and relatively well sclerotised, as in *C. crypticus*. Blind duct (*D.O.*) small.

Records.—Description and drawings of female (R.T. No. B19350-1) from same host and general locality as holotype—*viz. Hylomys suillus*, Mt. Kinabalu, Mari Parei, elev. 4900 ft., 24.viii.1953 (*R. Traub*). Also : one male, *ibid.*; one female, *ibid.*, but 26.viii ; one female, *ibid.*, but *ex Tupaia montana*, 24.viii ; one female, *ibid.*, but *ex Hylomys suillus*, Tenompak, 4500 ft. (the exact type locality), 19.viii; one male as the last but 11.viii.

Comment on the genus *Cratynius*.

Both *Cratynius crypticus* sp. n. and *C. audyi* (Traub, 1952) seem to be scarce, or at least were very difficult to collect in the climatic periods during which the joint U.S. Army-British Colonial Office Medical Research Units operated on Mt. Kinabalu on three occasions.[3] In fact, despite the intensive collecting of small mammal hosts by these Units, it was only during the third expedition that the missing sex of each species was found. The four known specimens of *C. crypticus* were taken from two *Hylomys suillus* and one *Rattus alticola*. *C. audyi* is known from only nine specimens collected from seven *Hylomys suillus* and one *Tupaia montana*. On the other hand, 46 *Hylomys*, 91 *Tupaia montana* and 87 *Rattus alticola* were very carefully searched for ectoparasites. Of these at least one-fourth of the *Hylomys* had been captured alive or had been recently killed prior to collection, so that one would reasonably presume that the fleas parasitising these hosts would still be on the animal at the time of examination. At least half of the other hosts were taken alive or were in excellent condition when searched for ectoparasites. The *Tupaia* and *Rattus* provided hundreds of fleas of other species, as well as myriads of mites, while the *Hylomys* invariably were very heavily infested with trombiculid mites, indicating that the techniques of collection and examination were satisfactory.

It is doubtful that there is a true seasonal variation of abundance of *Cratynius* in North Borneo, because there are no seasons *per se* on Kinabalu. However, there are indefinite short periods of light, brief rains as compared with daily heavy rainfall which is characteristic of the greater part of the calendar year. The field units operated in the Tenompak area during three periods of relative drought, but it nevertheless rained at least briefly nearly every day. Another possible explanation for the apparent dearth of *Cratynius* is that these fleas leave the host very readily as soon as it is disturbed, as is the case for some Borneo laelaptids. Or they may be nest-fleas, which leave the host for the shelter of the nest or run immediately after feeding.

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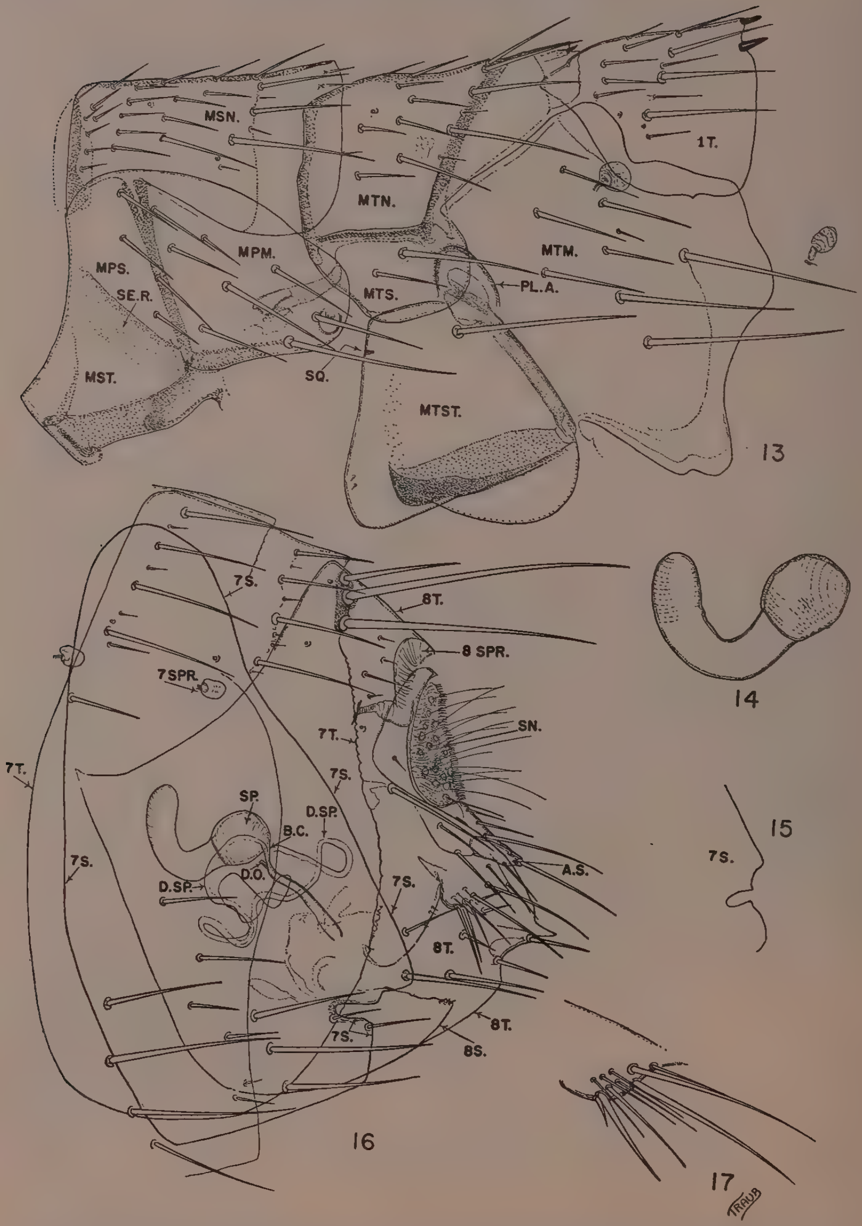
[3] The same seems to be true of *C. bartelsi* Jordan, 1933. There are only two specimens of this Javanese species in the collection of the British Museum (Nat. Hist.), one obtained from *Hylomys suillus*, and the other from *Rattus bartelsi*.


MSN.
1T.
MTN.
MPM.
MPS.
MTM.
SE.R.
MTS.
PL.A.
MST.
SQ.
MTST.
13
7S.
8T.
8 SPR.
7SPR.
SN.
7T.
7T.
7S.
SP.
D.SP.
B.C.
7S.
D.O.
D.SP.
7S.
A.S.
8T.
8T.
7S.
8S.
14
15
7S.
16
17
TRAUB

FIGS. 13–17.—*Cratynius audyi* (Traub). (13) Meso- and metathorax. (14) Spermatheca. (15) Variation—seventh sternum, female. (16) Modified abdominal segments, female. (17) Ventral anal lobe.

c. COMMENT ON THE STATUS OF LEPTOPSYLLINAE AND AMPHIPSYLLINAE.

The description of *C. audyi* (Traub, 1952) was followed by a characterisation of the Leptopsyllinae and a discussion of its status. Similarities with the Amphipsyllinae and differences from this subfamily were also pointed out (Traub, 1952). The discovery of the female of *C. audyi* and of *C. crypticus* sp. n. emphasises these points. *C. audyi* was stated to differ from typical Leptopsyllines in the following : (1) Absence of a genal comb ; (2) reduction of the tibial " comb " to the point where it is inapparent ; (3) presence of a distinct eye ; (4) with five pairs of lateral plantar bristles on ultimate segment of tarsi instead of the first pair being displaced ventrad. To these characters must now be added the fact that the two sexes of *Cratynius* differ markedly regarding the degree of development of the inter-antennal sulcus—the female is clearly integricipit, but the male is weakly fracticipit (as much so as *Peromyscopsylla* I. Fox, 1939, a typical Leptopsylline). In view of these morphological characteristics of *Cratynius*, apparently all that remains to separate the Leptopsyllines from Amphipsyllines are : (1) In Leptopsyllinae the sterno-episternal ridge of the mesothorax is sclerotised throughout, whereas in Amphipsyllinae it is sclerotised only posteriorly or not at all. (2) In male Leptopsyllinae there is an intimate connection between the crochet of the phallosome and the apical arm of the ninth sternum. (Either the distal portion of the apical arm of the ninth sternum is band-like and surrounds the crochet, or a lobe of the latter grips the outer side of the apical arm of the ninth sternum.) In the Amphipsyllinae there is no such connection between the phallosome and the ninth sternum. (3) Leptopsyllinae are nearly always fracticipit (*Cratynius* females being the exception) and Amphipsyllinae integricipit.

List of abbreviations.

*A.A.*9, Apical arm of male ninth sternum.
A.B., Antepygidial bristle.
*AP.R.*9, Apodemal rod of male ninth sternum.
AP.S., Sclerites of apodemal strut.
A.S., Anal stylet.
*B.A.*9, Basal arm of male ninth sternum.
B.C., Bursa copulatrix.
B.I.T., Band of inner tube.
CR., Crochet of phallosome.
C.S., Crescent sclerite of phallosome.
D.O., Ductus obturatus.
D.SP., Blind duct or duct of spermatheca.
F., Movable process or finger of clasper.
I.R., Ventral intramural rod of endophallus.
L.P., Labial palp.
M.D.L., Median dorsal lobe of phallosome.
MPM., Mesepimeron.
MPS., Mesepisternum.
MSN., Mesonotum.
MST., Mesosternum.
MTM., Metepimeron.
MTN., Metanotum.
MTS., Metepisternum (" lateral metanotal area ").
MTST., Metasternum.
P., Fixed, or immovable, process of clasper.
PL.A., Pleural arch of metathorax.
P.R., Penis rods of phallosome.
P.S., Proximal spur of phallosome.
P.W., Wall of aedeagal pouch.
RG., Pale ring above ventral margin of antennal groove.
SE.R., Sterno-episternal ridge of mesothorax.

List of Abbreviations—(contd.)

S.I.T., Sclerotized inner tube of phallosome.
SN., Sensilium.
SP., Spermatheca.
SQ., Squamulum.
T.A., Anterior tentorial arm of endoskeleton.
TB., Frontal tubercle.
V.A.L., Ventral anal lobe of female.
*VC.*1, First link-plate or " vinculum "
1*T.*, First tergum.
7*S.*, Seventh sternum.
7*SPR.*, Spiracle of seventh segment.
7*T.*, Seventh tergum.
8*S.*, Eighth sternum.
8*SPR.*, Spiracle of eighth segment.
8*T.*, Eighth tergum.

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ZUR TERMINOLOGIE DER TAXONOMISCH BEDEUTSAMEN ÄUSSEREN GENITALORGANE DER FLÖHE (SIPHONAPTERA).

Von F. Peus.

(*Zoologisches Museum der Humboldt-Universität Berlin.*)

Mit 7 Figuren.

Auf dem IX. Internationalen Kongress für Entomologie in Amsterdam ist Herr Prof. Dr. S. L. Tuxen, Kopenhagen, beauftragt worden, ein von ihm dort vorgeschlagenes *Glossary of terms of outer genitalia in Insects* zu redigieren und herauszugeben. Bei der Bearbeitung der Flöhe, die Herr Tuxen mir für dieses Werk übertragen hat, erwies es sich als nützlich, für einige Organe oder Strukturen neue Termini vorzuschlagen und einzusetzen. Herr Tuxen verfolgt in seinem Glossary aber den Grundsatz, dort keine Originalschöpfungen zu bringen, sondern nur schon publizierte Darlegungen zu referieren.

Nachdem The Honourable Miriam Rothschild, Ashton Wold, Peterborough, und Mr. Harry K. Clench, Pittsburgh, mich liebenswürdigerweise eingeladen haben, mich mit einem Beitrag aus der Flohkunde an der *Festschrift* zu Ehren von Herrn Dr. H. E. Karl Jordan zu beteiligen, scheint es mir, indem ich dieser Einladung gern folge, passend zu sein, diesen Beitrag mit der Anregung Tuxens zu verbinden, die darauf abzielt, meine Vorschläge für die Terminologie der Genitalorgane der Flöhe vorweg an anderer Stelle zu bringen, die im Glossary sodann zitiert werden könne.

Ich möchte es nicht unterlassen, meine Freude darüber auszudrücken, dass es mir vergönnt ist, auch durch die Beteiligung an der Festschrift Herrn Dr. Jordan, dem erfolgreichsten und verdienstvollsten Erforscher der Flöhe und Senior unter den Siphonapterologen, meine Verehrung und Bewunderung darbringen zu können. Mit dem vorliegenden Thema glaube ich ihm um so mehr aufwarten zu dürfen, als Dr. Jordan bei seinem Anliegen, die Taxonomie vergleichend morphologisch zu betreiben, gerade auch den Genitalorganen der Flöhe grösste Beachtung geschenkt und entscheidend daran mitgearbeitet hat, sie terminologisch zu erschliessen und diagnostisch zu verwenden.

Eine Terminologie ist *keine* Morphologie. Das Ideal wäre zweifellos eine Terminologie, die auf einer morphologischen Homologisierung der einzelnen Organe und Strukturen unter allen Floh-Gattungen insgesamt fusst. Die Lösung dieser Aufgabe liegt heute aber noch fern. Für die Taxonomie und Diagnostik bis in die Differenzierung von Subspezies hinein ist nämlich beim ♂ ausser den äusseren Bildungen der modifizierten Segmente auch das Phallosom von wesentlicher, bisweilen ausschlaggebender Wichtigkeit. Das Phallosom, in ihm vor allem der Aedoeagus, ist bei den Flöhen aber ein äusserst kompliziertes Gebilde, das im ganzen Insektenreich seinesgleichen sucht. Die neuerdings tatkräftig und erfolgreich begonnene morphologische Analyse des Aedoeagus (Wagner, Snodgrass, besonders auch Jordan, und sehr eingehend Traub) hat nicht nur einen Einblick in die verblüffende strukturelle Komplizierung gewährt, sondern auch eine hohe Mannigfaltigkeit in der Formabwandlung wie auch in der Ausbildung eigener, spezifischer Strukturen im Vergleich verschiedener Gattungen miteinander ersichtlich gemacht. Das aber nötigt uns Zurückhaltung in der Entwicklung einer Terminologie auf, bis die Ausdehnung derartiger Untersuchungen möglichst auf alle, jedenfalls aber auf sehr viel mehr Gattungen als bis heute geschehen, eine Homologisierung und damit eine auch morphologisch gerechte Terminologie der Einzelteile ermöglichen wird. Zweifellos erheischt die Kompliziertheit des Aedoeagus für viele seine Strukturen eine eigene, den Flöhen reservierte Terminologie.

In der Wahl der Termini habe ich mich—eine Selbstverständlichkeit—von weitestgehender Pietät vor eingebürgerten, gebräuchlichen Bezeichnungen leiten lassen, wo immer ihre Eindeutigkeit befriedigend ist. Dabei sah ich auch keinen Grund, einen schon international gebräuchlichen Terminus etwa deswegen zu verwerfen, weil er einer modernen Sprache entnommen ist; z.B. entsprechen Bezeichnungen wie "Clasper" oder "Finger" durchaus allen Anforderungen, die an einen echten Terminus zu stellen sind.—Als Instrumente der Wissenschaft sind Termini jedoch für den *internationalen* Gebrauch bestimmt. Ich habe es daher vorgezogen, eine Anzahl von Ausdrücken, die bisher nur in einer modernen Sprache (englisch) existieren, zu latinisieren; da dies jedoch in Form wörtlicher, gleichsinniger Übersetzung geschehen ist, bleibt zugleich der Grundsatz der Pietät gewahrt, z.B.: heel (Jordan, Traub) = Calx; keel (Traub) = Carina; girdle (Traub) = Cingulum; neck (Traub) = Collum; crescent sclerite (Traub) = Lunarsklerit (lunar sclerite); inner tube (Snodgrass) = Tubus interior; sail (Traub) = Velum, etc. Doch bin ich den Weg der Latinisierung nicht konsequent bis zu Ende gegangen; für manche verbliebene modern-sprachige Bezeichnungen mögen sich mit der Zeit treffende und geeignete Termini von selber noch finden.—Weiterhin sind Termini in erster Linie Mittel des *Gebrauchs*. Wie die Gebrauchsgegenstände des täglichen Lebens möglichst zweckmässig und "handlich" sein sollen, müssen wissenschaftliche Termini, bei aller Wahrung sachlicher Exaktheit und Präzision, ebenfalls möglichst einfach und knapp sein. Daher schien es mir geboten, einerseits schon bestehende echte Termini durch Verkürzung einfacher zu gestalten (z.B. Ductus seminalis communis [Snodgrass] = Ductus communis, wobei die Bezeichnung "seminalis" für einen weiblichen Organismus ohnehin nicht glücklich ist), andererseits aber auch solche Bezeichnungen, die (zumeist überdies in einer modernen Sprache) ein Organ mit mehreren Worten mehr beschreiben als benennen, durch neue knappe Termini zu ersetzen, z.B. penis rods (Snodgrass, Traub), copulatory rods (Sharif), levers of penis, Apophysen des Penis = Endotendons; apodemal rod of endophallus (Snodgrass), aedeagal apodemal rod (Traub) = Hypotendon; intramural rod of endophallus (Snodgrass) = Virga, etc. In einem Falle, in dem bisher eine Bezeichnung (Appendix) wechselnd für zwei verschiedene Teile desselben Organs (für Hilla und Papilla) verwendet wird, ist eine eindeutige Klarheit auch nur durch neue Termini herzustellen (Bulga, Hilla und Papilla der Spermatheke); die bisherige Bezeichnung der Bulga als "Reservoir" ist überdies insofern unglücklich, als auch die Hilla (bisher Appendix) der Speicherung des Spermas dient. Schliesslich boten sich neue Termini von selbst für solche Bildungen an, denen es noch an einer Bezeichnung überhaupt mangelt (das Epitendon am Aedoeagus-Apodem, die Fistula des Tubus interior, die Ruga des Velums, die Strigillin der Spermatheke). Die Schaffung von besonderen

Termini findet dort ihre Grenze, wo, wenigstens nach dem augenblicklichen Stande der Dinge, für die Praxis kein Bedürfnis vorliegt. Die Fortschritte in der morphologischen Analyse und Deutung und die Verfeinerung in der taxonomischen Auswertung werden sicher in Zukunft zu einem derartigen, Bedürfnis führen, z.B. besonders für die Strukturen des Aedoeagus; man wird dann aber die Einführung entsprechender Termini getrost auch der Zukunft überlassen können. Ich habe überhaupt meine Aufgabe nicht darin gesehen, alle bei den Flöhen vorkommenden Genitalstrukturen aufzuführen, sondern ich hielt es für ratsamer, mich auf einen Grundstock von den für die Taxonomie am meisten bedeutsamen Organen und Strukturen zu beschränken, für deren Terminologie eine stabile Konvention am vordringlichsten ist. In den morphologischen Darlegungen habe ich mich dabei eng an Snodgrass (1946) angeschlossen.

Eine Terminologie muss international einheitlich sein. Eine Einheitlichkeit kann aber nur auf dem Wege der freien Konvention zustandekommen. Mag daher der Hinweis, dass ich die hier neu geschaffenen Termini, wie die gesamte Terminologie überhaupt, nur als Vorschläge aufgefasst wissen möchte, auch überflüssig sein, so möchte ich dies ausdrücklich zu betonen doch nicht unterlassen.

Den Herren G. H. E. Hopkins und Frans G. A. M. Smit, beide in Tring, statte ich auch hier meinen herzlichsten Dank ab für die Liebenswürdigkeit, mit der sie meinen terminologischen Entwurf durchgesehen und mir Anregungen und Rat erteilt haben! Die Termini "Bulga" und "Hilla" für die Teile der Spermatheca gehen auf den Vorschlag von Herrn Smit zurück, den ich gern angenommen habe.

I. DIE TERMINOLOGIE DER GENITALORGANE DES ♂.

Von den 10 Abdominalsegmenten sind das VIII. und IX. Segment modifiziert. Das IX. Segment ist das Genitalsegment.

Segment VIII.

Das Tergum (*T*) kann gross (z.B. Ceratophyllidae) oder klein (z.B. Pulicidae) sein; im ersteren Falle ist es zuweilen in seiner Medianlinie gespalten. Die so entstandenen, nunmehr seitlich liegenden Tergalplatten tragen dann z.B. bei manchen Ceratophyllinae entlang ihrem Dorsalrande auf der Innenseite ein Feld von dichten, feinen Dörnchen, die Area spiculosa. Die Grösse des Sternums (*St*) steht meist im umgekehrten Verhältnis zu derjenigen des Tergums. Daher ist es z.B. bei den Ceratophyllidae lang und sehr schmal unter verschiedener Modifizierung vor allem seines distalen Teiles, bisweilen aber weiter reduziert oder gar rudimentär. Läuft es caudad in einen einheitlichen schmalen Arm aus, so kann es an seinem Ende ein Paar von aufwärts gerichteten membranösen Anhängen, die Apikalmembranen (*ap Memb*, fig. 6), und ausserdem die Apikalborsten (Setae apicales) (*ap Set*, fig. 6), in verschiedener Zahl und Form tragen. Die Intersegmentalhaut zwischen den Sterna VIII und IX kann beiderseits in einen mehr oder weniger grossen, verschieden geformten Lappen mit feiner Bewimperung oder Bedornung ausgezogen sein, die Intersegmentallappen (Lobi intersegmentales) (*L int*, fig. 6); in solchen Fällen befindet sich jederseits am basalen Ast des Sternums ein birnen oder pilzförmiges Organ, das Wagner'sche Organ (*WO*, fig. 6), das zweifellos eine Drüse darstellt, und mit dem die Intersegmentallappen wahrscheinlich in funktionellem Zusammenhang stehen.

Segment IX.

Das Tergum (*T*) ist bei allen Flöhen (♂) sehr stark modifiziert, indem es zu einem das ♀ bei der Kopulation festhaltenden Klammerapparat ausgestaltet ist (diese Funktion wird oft durch das ebenfalls entsprechend modifizierte Sternum IX noch unterstützt). Der Bau des Tergalkomplexes mag am Beispiel der Figuren 1, 2 und 4 verdeutlicht werden. Das Tergum im eigentlichen Sinne ist immer, wenn auch in verschiedenem Grade, bisweilen nur noch bis zur Andeutung, reduziert und immer ohne Haare und Borsten; seine gewöhnliche Form gleicht einem schmalen, jochartigen Band. Die einzelnen Teile des gesamten, auffälligen Tergalkomplexes sind also nur akzessorische Bildungen des im Vergleich zu ihnen verschwindend geringen morphologischen Tergums. Cephalad geht vom Tergum ein Apodem ab, dessen Grösse und Form bei den einzelnen Gattungen sehr variabel und bisweilen auch in zwei seitliche Platten aufgeteilt ist, das Tergal-Apodem (*t Ap*, figs. 1, 2, 4). Dem Tergum hängt der Haftapparat, der Clasper (*Cl*, figs. 1, 4) an (vgl. auch Fussnote p. 271); jede Hälfte dieses paarigen Organs ist mit dem unteren (seitlichen) Ende des Tergums, meist auch mit dem Tergal-Apodem verbunden, und beide Hälften zusammen bilden eine Zange oder Greifklammer, die der oben genannten Funktion dient. Am Clasper unterscheiden wir (1) seinen Hauptteil, den Corpus des Claspers (Clasper-Körper) (*Corp Cl*, figs. 1, 4), (2) ein an der vorderen, unteren Ecke entspringendes, cephalad gerichtetes Apodem von oft beträchtlicher Länge und Breite, das Manubrium (*M*, figs. 1, 2, 4) und (3) ein bewegliches Anhangsglied am Hinterrand des Corpus, den Finger (auch einfach als *F* bezeichnet, figs. 1, 2, 4); bei manchen Flöhen sind jederseits zwei Finger vorhanden. Der Finger kann am Dorsalrand mit Sinnesborsten, Sensillen (*Sens*, fig. 4) versehen sein. Der Corpus kann an seiner distalen oberen oder an seiner distalen unteren Ecke, bisweilen sowohl oben als auch unten, einen Fortsatz, Processus (*P*), haben, der in der Regel ein nicht beweglicher fester Auswuchs des Corpus ist. Im einen Falle ist es der Processus dorsalis (*dP*,

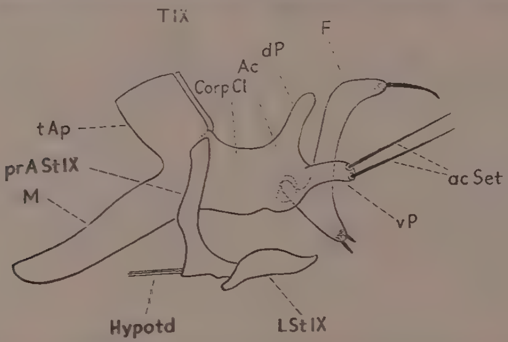

Fig. 1.—Tergum und Sternum IX (nur die linke Seite) von *Opisodasys* (Ceratophyllidae).

figs. 1, 2, 4), im anderen der Processus ventralis (*vP*, fig.s 1, 2). Der Dorsalprozess kann seinerseits durch einen Einschnitt in zwei sekundäre Zapfen aufgeteilt sein, und weiterhin kommt es vor, dass der untere von diesen beiden Sekundärzapfen wiederum durch einen Einschnitt gegabelt ist. In solchen Fällen mögen künftig diese Zapfen, da sie ja sämtlich aus sekundärer Teilung hervorgegangene Produkte desselben Fortsatzes (*dP*) sind, durch Bezifferung ihres Symbols *dP* bezeichnet werden, also als dP^1, dP^2 etc. (fig. 4).

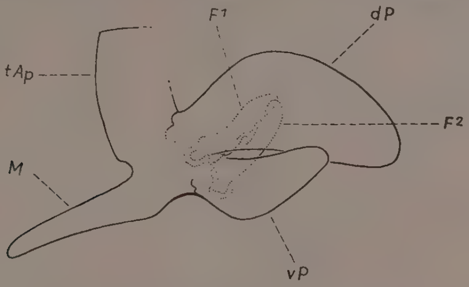

FIG. 2.—Clasper (nur die linke Seite) von *Cediopsylla* (Pulicidae).

Entsprechend der Art ihrer Verbindung mit dem Corpus werden beiderlei Anhangsgebilde (Finger und Fortsätze) in umständlicher Weise auch als " beweglicher Fortsatz (Finger) " und " unbeweglicher Fortsatz (Finger) " bezeichnet. Die Literatur bietet aber in der Terminologie oder Symbolisierung dieser Anhangsgebilde eine beträchtliche Uneinheitlichkeit dar. Ich glaube, dass eine klare und stabile Terminologie ohne Verstoss gegen morphologische Homologien, soweit sie schon gesichert sind, leicht erreicht werden kann, indem man, wie oben vorgeschlagen, die primär unbeweglichen Fortsätze als Processus und symbolisiert als *P*, die primär beweglichen Fortsätze aber immer als Finger und symbolisiert als *F* bezeichnet. Unter den Processus (*P*) braucht dann nur nach ihrer Lage zwischen Dorsalprozess (*dP*) und Ventralprozess (*vP*) unterschieden zu werden; wo eine sekundäre Aufspaltung des Dorsalprozesses vorkommt (vgl. fig. 4), werden die Teilfortsätze beziffert, ohne dass durch diese an das Symbol, *dP* gebundenen Ziffern eine Verwechslung mit anderen Anhängen auftreten kann. Auf die Tatsache, dass der Dorsalprozess und bisweilen auch noch der Ventralprozess sekundär beweglich geworden sein können (z.B. Pulicidae, vgl. fig. 2), braucht ihre Determinierung als eigentliche Processus (*P*) keine Rücksicht zu nehmen. Die Finger artikulieren immer primär beweglich am Clasper-Corpus; sind ihrer zwei vorhanden, so sollte man ungeachtet einer späteren Entscheidung, welcher von ihnen dem in anderen Gattungen nur einzigen Finger homolog ist, einfach topographisch den oberen als F^1 und den unteren als F^2 bezeichnen (fig. 2). Ist nur 1 Finger vorhanden, so lautet seine Bezeichnung einfach nur *F*.

Die Insertionsgrube des Fingers heisst Acetabulum (*Ac*, fig. 1). Die in ihrer Nähe am Corpus-Hinterrand stehenden, meist kräftigen Borsten heissen danach Acetabularborsten (*ac Set*, fig. 1); diese kommen jedoch nur bei einem Teil der Flöhe vor.

Das Sternum (*St*) ist immer stark modifiziert und kann die verschiedenste Gestalt haben. Im typischen Falle (fig. 4) besteht es aus einem horizontal liegenden einheitlichen Distalarm (*di A*), von dem winklig nach vorn-oben zwei, die Basis des Clasper-Körpers umgreifende lange Gabeläste, die Proximalarme (*pr A*) abzweigen. Oft ist aber auch der Distalarm gabelförmig gespalten (z.B. *Ceratophyllus*; in der fig. 6 ist freilich nur der dem Beschauer zugekehrte linke Ast dargestellt). In solchen Fällen kann jeder Distalarm 2 oder 3 Lappen ausbilden, die Lobi (des Sternums IX), die man mit Anhangsziffern als L^1, L^2 und L^3, von der Spitze zur Basis gezählt, differenzieren kann. Die beiden Distalarme umschliessen an ihrem Grunde die Aedoeagus-Tasche (*aed Pch*, figs. 6, auch 3, 5), aus der die Aussenwandung des Aedoeagus hervorgeht. Es gibt hier eine Sehne von verschiedener Stärke, die sich immer unterhalb des Endophallus in horizontaler Richtung verschieden weit nach vorn (cephalad) hinzieht. In manchen Fällen (z.B. Ceratophyllidae, fig. 6) entspringt sie am Sternum IX dort, wo es sich in die beiden Proximalarme teilt; in anderen Fällen aber ist sie, die Sternum-Gabel passierend, unten an der Aedoeagus-Tasche (z.B. Pulicidae, fig. 3, *Ctenophthalmus*, fig. 5), bisweilen auch am Aedoeagus selbst angeheftet. Ungeachtet ihrer Ursprungsstelle möge sie, weil sie von allen im Phallosom vorhandenen Sehnen die unterste ist, topographisch als das Hypotendon (*Hypotd*, figs. 1, 3, 4, 5, 6) bezeichnet werden.

Phallosom.

Das einführende Organ, das Phallosom, ist von bedeutendem taxonomischen Interesse. Die Teile, aus denen es besteht, sind: (1) Der caudad nach aussen gerichtete Aedoeagus (*Aed*), normalerweise oberhalb des Distalarms des Sternums IX gelegen; (2) das mehr oder weniger breite Aedoeagus-Apodem (*aed Ap*), das vom Aedoeagus entspringend horizontal nach vorn (cephalad) in das Abdomen, oberhalb des Endophallus, hineinreicht, und (3) der Endophallus (*Enph*), ein weichhäutiges, sack- oder schlauchförmiges Gebilde, das, vom Aedoeagus ausgehend, sich ebenfalls weit nach vorn ins Abdomen hinein erstreckt, an seinem dortigen vorderen Ende aufwärts gebogen ist und hier den Ductus ejaculatorius aufnimmt.

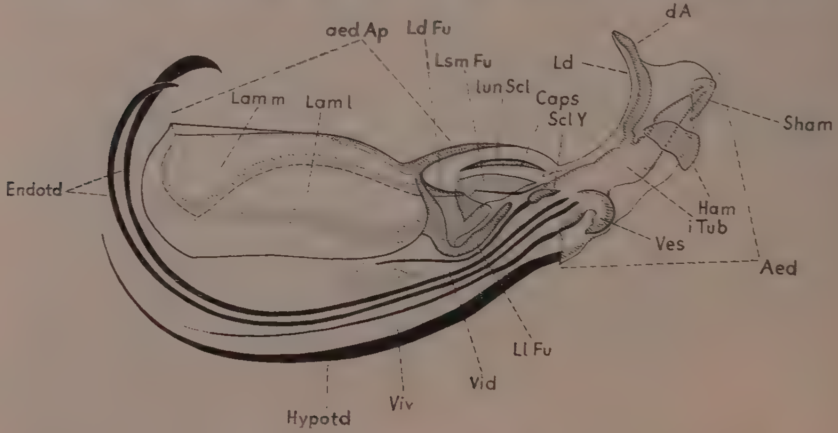

Fig. 3.—Phallosom von *Ctenocephalides* (Pulicidae).

Aedoeagus.—Am Ende des Aedoeagus ist durch Einstülpung von hinten her ein weiter Hohlraum, die Endkammer entstanden, die nach hinten und gleichzeitig in verschiedenem Umfang auch nach unten weit geöffnet ist. Die Umwandung der Endkammer repräsentiert die wahren Parameren[1]. Der Rand der Öffnung (Gonotreme, *Gtr*) ist gewöhnlich in mehrere Lappen oder Lobi (*L*) aufgeteilt, die in ihrer Zahl, Grösse und Form bei den einzelnen Gattungen sehr wechseln und in der Literatur die verschiedensten Bezeichnungen erhalten haben. Vorläufig dürfte es genügen, die folgenden beiden Lobi zu unterscheiden: Distal über der Gonotreme liegt der Dorsallobus (*Ld*, figs. 3, 5, 6), er kann einfach oder paarig sein, im letzteren Falle kann jeder Teillappen seinerseits einfach oder in zwei oder mehr Teile aufgespalten oder sonstwie modifiziert sein. Der Rand des unteren Teiles der Endkammeröffnung kann die Laterallobi (*Ll*, figs. 4, 5, 6) ausbilden, die also, wenn sie vorhanden sind, die Gonotreme beiderseits flankieren, ausserdem aber auch mehr oder weniger weit nach vorn verlängert sein können; auch sie können in Form und Grösse artspezifisch ausserordentlich variieren. Die paarigen Dorsallobi können an ihrem Endrande durch die Apikalsklerite (*ap Scl.* figs. 4, 5) und

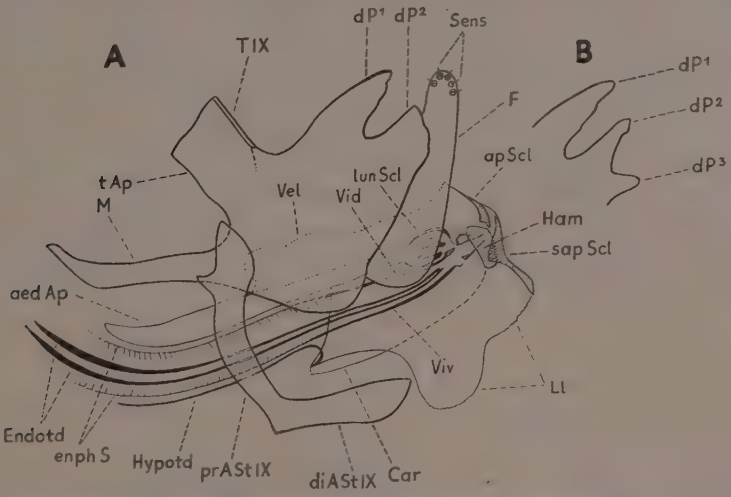

FIG. 4.—(A) Segment IX und Phallosom von *Ctenophthalmus agyrtes* ssp. (Hystrichopsyllidae). (B) Der dreigeteilte Dorsalprozess des Clasper-Körpers bei anderen Subspezies von *Ct. agyrtes* (der dP^2 ist untergeteilt in dP^2 und dP^3).

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[1] In dieser Deutung folge ich Jordan (vgl. auch Hopkins & M. Rothschild, 1953). Snodgrass (1946) glaubt, dass die Parameren zu den Claspers geworden sind. Wenn, unabhängig von dieser Frage, die Claspers, wie Snodgrass es deutet, den Basimeren und Distimeren („ Coxiten " und „ Styli " der „ Gonopoden ") anderer Insekten homolog sind (sie entsprechen ihnen jedenfalls funktionell), so ergibt sich die bemerkenswerte Tatsache, dass die Flöhe denselben Effekt, den z.B. manche Dipteren in individueller Wiederholung durch die Torsion des Hypopygs erreichen (nämlich die Verlangerung der sternalen „ Gonopoden " in die Dorsallage), durch die (sekundäre ?) Anlagerung der „ Gonopoden " an das Tergum endgültig stabilisiert haben, also unter Verzicht auf eine Torsion der Terminalia, die wegen der lateralen Komprimierung der Segmente technisch denn auch nicht möglich wäre.

ebenso die Laterallobi distal durch die Subapikalsklerite (*sap Scl*) verstärkt sein (z.B. bei *Ctenophthalmus* s. str., fig. 4, vorhanden; beim Subgenus *Euctenophthalmus*, fig. 5, zwar durch die Umrissform des Lobus angedeutet, aber nicht als Sklerit differenziert). Im Anschluss an den Dorsallobus kann die Dorsalwand des Aedoeagus nach vorn mehr oder weniger stark aufgebläht sein, bisweilen in Form einer mächtigen " Dorsalblase " (fig. 5, *aed dW*), deren vordere Kante dann von einer feinen Falte, der Ruga (*R*, fig. 5), umrundet sein kann; der oft noch weiter nach vorn reichende, dem Aedoeagus-Apodem aufliegende, mässig aufgewölbte Teil der Dorsalwand wird als das Velum (*Vel* figs. 4, 5) bezeichnet.—Die Verbindung der Wände der Aedoeagus-Tasche in der Ventrallinie kann als Carina (*Car*, figs. 4, 5) sklerotisiert sein, und auch der senkrechte Vorderrand dieser Tasche kann in Form einer schmalen sklerotisierten Leiste, Cingulum (*Cing*, fig. 5), verstärkt sein, die nach oben die Basis des Aedoeagus mitsamt seinem Apodem umgreift und sich bisweilen, seitlich in scharfem Winkel nach hinten umknickend, auch noch in der Wand der Aedoeagus-Tasche mehr oder weniger weit nach hinten zwischen den Laterallobi fortsetzt (*Cing'*, fig. 5).—Der Endophallus setzt sich nach hinten in den sklerotisierten Tubus interior (*i Tub*, figs. 3, 5) fort. Dieser durchläuft den Aedoeagus

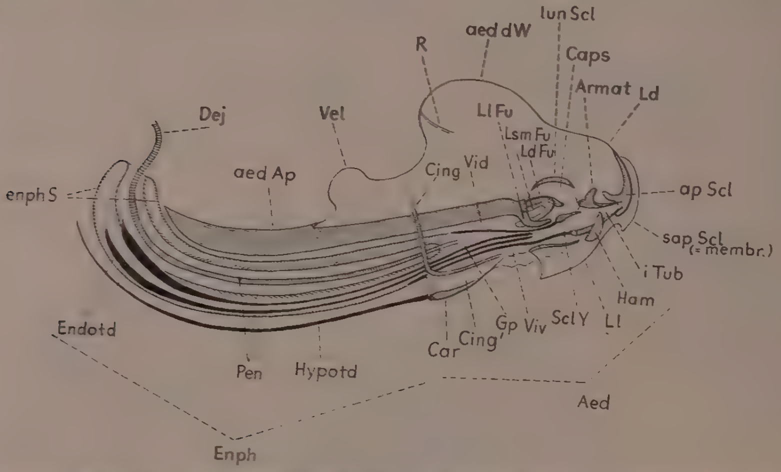

Fig. 5.—Phallosom von *Euctenophthalmus* (Hystrichopsyllidae). Endophallus halbschematisch.

in seiner Längsachse und ragt hinten als freies Rohr in die Endkammer hinein; da er hier durch eine Ausstülpung des Bodens der Endkammer gebildet ist, stellt seine Mündung also die eigentliche Öffnung des Aedoeagus dar. Die Wandungen des frei in die Endkammer hineinragenden Teiles des Tubus zeigen, vor allem dorsal, spezifisch modifizierte Strukturen, die als die Armatur (des Tubus interior) (*Armat*, fig. 5) bezeichnet werden. Bisweilen hat der Tubus schräg nach hinten-oben gegen den Dorsallobus hin einen sklerotisierten Fortsatz, den Dorsalarm (*dA*, fig. 3); wenn dieser über den Aedoeagus frei nach aussen hinausragt (z.B. bei manchen *Xenopsylla*-Arten), wird er auch als " semi-detached rod " bezeichnet. Weiter nach vorn, gleich hinter den Lobi des Fulcrums, ist dorsal mit dem Tubus ein Hohlraum, die Capsula (*Caps*, fig. 3, 5), verbunden, die von einem im Profil meist wie die Mondsichel aussehenden Sklerit, dem Lunarsklerit (*lun Scl*, figs. 3, 4, 5, 6) überdacht wird. Ventral, der Capsula etwa gegenüber, bildet der Tubus an seiner Basis oft eine sklerotisierte halbkreisförmige Erweiterung aus, die Vesicula (*Ves*, fig. 3). Bei manchen Ceratophyllidae hat der Tubus interior nach aussen über die Endkammer hinaus eine lange, dünnwandige, schlauchförmige Verlängerung, die, so lange das ♂ noch nicht kopuliert hat, scharf unter den Aedoeagus nach vorn zurückgebogen ist und dort zwischen Aedoeagus und Sternum IX verborgen liegt. Dieser Tubus exterior mag kurz als Fistula (*Fist*, fig. 6) bezeichnet sein. Das Ende des Tubus interior kann von einem Paar flach scheibenförmiger, im Umriss aber sehr verschieden geformter Anhänge (sklerotisiert oder membranös) flankiert sein, die an der Innenwand der Endkammer inserieren und ein wenig beweglich sind ; sie sind vielfach als " Parameren " (in Wirklichkeit sind sie nur Anhangsbildungen, also nur Derivate der eigentlichen Parameren, s.o.), in der angelsächsischen Literatur auch als " crochets " bezeichnet, doch erscheint es als glücklicher, sie altsprachig Hamuli (*Ham*, figs. 3, 4, 5, 6) zu nennen. In manchen Fällen, z.B. bei Pulicidae (fig. 3) kann distal von ihnen noch ein zweites Paar ähnlicher Sklerite liegen, die somit Subhamuli (*Sham*, fig. 3) heissen mögen.

Aedoeagus-Apodem.—Dieses grosse Apodem (bisher auch Penisplatte genannt) besteht aus drei langgestreckten Blättern, den Laminae (*Lam*) : Die Lamina media (*Lam m*, fig. 3) steht median senkrecht, flankiert beiderseits von den Laminae laterales (*Lam l*) derart, dass sie oben mit dem Dorsalrand der Lamina media verwachsen sind und von dort in flacher Wölbung seitlich nach unten herabhängen. Die mediane Lamina ist nach hinten (caudad) verlängert und bildet hier das Fulcrum (*Fu*, fig. 6), das mit seinen drei paarigen Fortsätzen die Basis des Tubus interior umgreift und diesem als Stütze und Führung dient. Die drei Fortsatzpaare können als dorsale, submediane und laterale Lobi (des Fulcrums) (*Ld*, *Lsm*, *Ll Fu*, figs. 3, 5) bezeichnet werden. Bisweilen sind die apodemalen Laminae laterales an ihrem distalen Ende, den Endophallus umgreifend, nach unten erweitert und vereinigen sich in der Ventrallinie zum sogenanten Calx (" heel " bei Traub 1950, vgl. dort Taf. 38 fig. 5 und 6, Gattung *Polygenis*). Unmittelbar vor dem Fulcrum kann die Lamina media eine halsartige Einschnürung, das Collum (*Coll*, fig. 6), aufweisen. Am proximalen Ende des Aedoeagus-Apodems (Lamina media) greift bisweilen eine Sehne an ; da sie die oberste aller Sehnen ist, die im Phallosom vorkommen können, schlagen wir für sie den Namen Epitendon (*Epitd*, fig. 6) vor.

Endophallus (vgl. fig. 5).—Die weichhäutige Aussenwandung, der Sack des Endophallus (*enph S*, fig. 4, 5), setzt sich nach hinten in den Tubus interior fort. In der dorsalen und ventralen Medianlinie ist die Wandung durch je einen dünnen sklerotisierten Strang verstärkt ; der dorsale mag als Virga dorsalis (*Vi d*), der untere als Virga ventralis (*Vi v*, figs. 3, 4, 5, 6) bezeichnet sein. Beide Virgae sind hinten an dem Tubus interior angeheftet, wobei die dorsale dort immer eine annähernd tropfen- oder spindelförmige Verdickung bildet ; dieser wechselnd grosse Sklerit mag in Vereinfachung der Sharif'schen Bezeichnung " Y-shaped dorsal sclerite " kurz Sklerit Y (*Scl Y*, figs. 3, 5) genannt sein. Die Virga ventralis erstreckt sich in der Regel weiter nach vorn als die dorsale (figs. 3, 5, 6). Am aufwärts gebogenen Vorderende stülpt sich der Endophallus-Sack nach innen ein, auf diese Weise eine bis zur Basis des Aedoeagus reichende Röhre bildend. Dieser nach aussen meist fein bewimperte innere Tubus des Endophallus ist seinerseits in seiner ganzen Länge vom Ductus ejaculatorius (*Dej*, fig. 5) durchzogen, der mit einer feinen Öffnung durch das verjüngte Ende des inneren Endophallus-Rohres frei gegen den Tubus interior hin ausmündet. Diese Mündung ist also die Gonopore (*Gp*, fig. 5), und somit ist der den Ductus ejaculatorius bergende innere Schlauch des Endophallus der wahre Penis (*Pen*, fig. 5). (Bei den Flöhen kann dieses Organ freilich nicht in die weiblichen Genitalorgane eingeführt werden, weil es für die Passage durch den Tubus interior des Aedoeagus viel zu dick ist.)

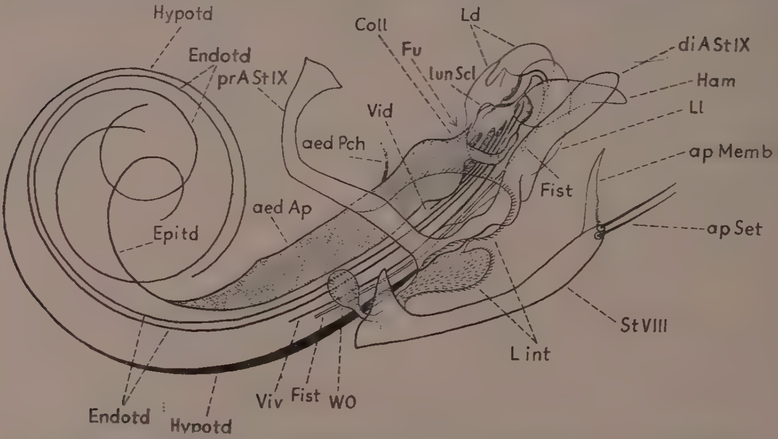

Fig. 6.—Sternum VIII und IX und Phallosom von *Ceratophyllus* (Ceratophyllidae).

Die Bezeichnung "Penis" wird in der Flohliteratur äusserst verschieden verwendet und meist auf Organe oder Organkomplexe bezogen, denen diese Bezeichnung weder im streng morphologischen noch funktionellen Sinne zukommt, z.B. für den Tubus interior, Aedoeagus, Endophallus oder gar für das ganze Phallosom. Das Penis-Rohr wird im Inneren des Endophallus-Sacks begleitet von einem Paar sklerotisierter Sehnen, die vorn, wo sie oft verbreitert sind, durch Muskeln mit der Wandung des Endophallus-Sacks verbunden sind; ihr Ende ragt in der Ruhelage über das Penis-Ende hinaus bis an die Basis des Tubus interior heran. Durch Betätigung ihrer basalen Muskeln werden sie bei der Copula nach hinten vorgestossen, und zwar durch den Tubus interior hindurch nach aussen; sie sind die einzigen Organe des ♂, die in das Ostium bursae des ♀ hineingeführt werden und das Sperma dorthin geleiten. Nachdem wir für die anderen Sehnen des Phallosoms kurze topographisch bestimmte Bezeichnungen gewählt haben (Hypotendon, Epitendon), schlagen wir in analoger Weise auch für diese "penis rods" (Snodgrass) nach ihrer Lage den Namen Endotendons (*Endotd*, figs. 3, 4, 5, 6) vor.

II. Die Terminologie der Genitalorgane des Weibchens (♀).

Von den 10 Abdominalsegmenten sind beim ♀ die Segmente VII bis IX modifiziert. Das VIII. ist das Genitalsegment.

Am Segment VII ist nur das Sternum modifiziert, das mit seinen oberen Teilen (auf der Körperseite) die unteren Teile des Tergums überlagert, im Gegensatz zum umgekehrten Verhalten der normalen Segmente. Der Hinterrand des Sternums hat meist trotz der Variabilität in gewissen Grenzen eine artspezifische Form und ist daher taxonomisch-diagnostisch sehr wichtig. Oft zeigt er eine verschiedene tiefe und bei den Gattungen und Arten charakteristisch geformte Einbuchtung, den Sinus (des Sternums VII), durch den dann zwei lappenförmige Vorsprünge des Hinterrandes entstehen, einer über und einer unter dem Sinus, die Lobi (des Sternums VII). Bisweilen gibt es auch zwei Sinus.—Am Segment VIII sind die Setae genitales (Genitalborsten) besonders differenziert in Form von kurzen, starren, dornförmigen Borsten auf der Innenfläche des Tergums nahe seinem Hinterrand.—Von den stark reduzierten Teilen des Segments IX, die bei den meisten Flöhen vom Tergum VIII ganz überdeckt sind, hat Lass (1905) das über der Genitalkammer liegende schwach sklerotisierte Sternum nicht als solches erkannt und daher als " Valvula vaginalis " bezeichnet.—

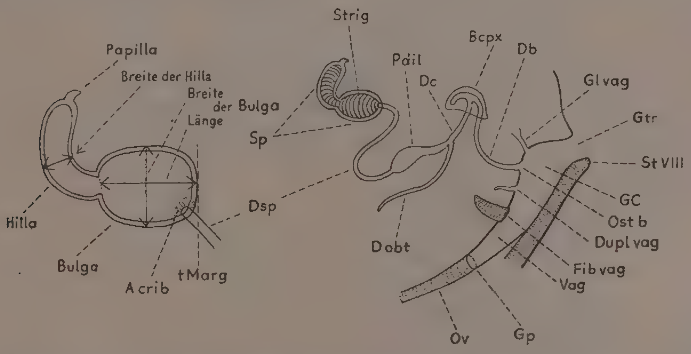

Fig. 7.—Die weiblichen Genitalorgane. Linke Nebenfigur: Spermatheke allein. Schema.

Die äussere Genitalöffnung, Gonotreme (*Gtr*, fig. 7), liegt unterhalb des Proctigers (Segment X), seitlich umschlossen von den Hinterrändern des Tergums VIII und unten abgegrenzt durch die Spitze des Sternums VIII. Sie führt in eine tiefe Höhlung, die Genitalkammer (*GC*), die somit ebenfalls seitlich von den hinteren Teilen des Tergums VIII, ventral vom Sternum VIII und dorsal von Sternum IX umgrenzt wird. Ihr innerer, sich verjüngender Teil ist die Vagina (*Vag*), in die von innen (vorn) her der Oviduct (*Ov*) einmündet; die Mündung des Oviducts ist die Gonopore (*Gp*). An der von aussen nach innen schräg zur Vagina hinabführenden Dorsalwand der Genitalkammer befindet sich oben zunächst die Ausmündung einer Drüse, der Glandula vaginalis (*Gl vag*), und ein wenig unter dieser der Eingang zur Bursa copulatrix, das Ostium bursae (*Ost b*); ein wenig tiefer tritt meist eine Querfalte, die Duplicatura vaginalis (*Dupl vag*), auf und wiederum unter dieser (oder statt ihrer) ein querliegender Sklerit, die Fibula vaginalis (*Fib vag*).—Vom Ostium bursae führt der Ductus bursae (*Db*) zur Bursa copulatrix (*B cpx*). Sind noch zwei Spermatheken vorhanden (bei wenigen Gattungen), so führen aus der Bursa zwei Ductus spermathecae (*D sp*) zu ihnen hin. Die meisten Flöhe haben aber nur noch eine Spermatheke; von der anderen ist dann gewöhnlich nur noch der zugehörige Ductus als ein blind endendes Rudiment erhalten geblieben, der Ductus obturatus (*D obt*). Dieser kann direkt aus der Bursa entspringen, er kann aber auch erst etwas weiter jenseits von ihr von dem intakten Ductus spermathecae abzweigen; der gemeinsame Teil des Ganges zwischen der Bursa und der Abzweigung heisst dann Ductus communis (*Dc*). Jenseits der Abzweigung ist der eigentliche Ductus spermathecae oft in verschiedener und artcharakteristischer Ausdehnung und Form zu der Pars dilatata (*P dil*) erweitert. Die Spermatheca (*Sp*) besteht immer aus zwei Abteilungen, aus der Bulga, in die der Ductus spermathecae einmündet (Ostium), und aus einem sich anschliessenden kleineren Teil, der Hilla. Die Hilla kann auf ihrer Spitze mit einem kleinen knopfartigen Vorsprung, der Papilla, versehen sein. Die feinen Furchen auf der Innenwand der Bulga, oft auch der Hilla, mögen als Strigillae (*Strig*) bezeichnet sein. Eine rings um das Ostium des Spermathekalganges sich meist deutlich abhebende Zone von sehr feinen Poren, durch die das Sekret von Drüsen in die Bulga gelangt, ist die Area cribriformis (*A crib*). Die der Basis der Hilla, die ja bezogen auf ihre Lage im Körper nach vorn (cephalad) gerichtet ist, gegenüberliegende Wand der Bulga ist ihr Terminalrand (*t Marg*). Als Längsachse (Länge) der Bulga gilt immer die Linie vom Terminalrand zur Basis der Hilla, auch dann, wenn die senkrecht zu ihr stehende Achse (Breite) tatsächlich die längere ist. Der Ductus spermathecae mündet meist in der Terminalwand (gegenüber der Hilla), oft aber auch an der Ventral- und selten an der Dorsalwand in die Bulga ein.

Erklärung der Abkürzungen in den Figuren
zugleich die wichtigste Synonymie (in Kursivdrack).

Ac	Acetabulum.
ac Set	Acetabularborsten, acetabular bristles.
A crib	Area cribriformis.
Aed	Aedoeagus, aedeagus.
aed Ap	Aedoeagus-Apodem, aedeagal apodeme. *Leitskelett* (Landois, 1866), *penis plate* (Jordan & Rothschild, 1908).
aed dW	Dorsalblase (Wagner 1940) (der Dorsalwand des Aedoeagus), enlargement of aedeagal dorsal wall.
aed Pch	Aedoeagus-Tasche, aedeagal pouch.
ap Memb	Apikalmembran (des St IX), apical membrane. *membranous appendage or flap, plume* (Hubbard, 1947).
ap Scl	Apikalsklerit (des Dorsallobus des Aedoeagus), apical sclerite (of aedeagal dorsal lobe).
ap Set	Apikalborsten (des St IX), apical bristles.
Armat	Armatur (des Tubus interior) armature (of sheath of inner tube). *Endapparat* (Wagner, 1940).
B cpx	Bursa copulatrix.
—	Bulga (Smit, i litt.). *body, head, reservoir of spermatheca.*
Car	Carina (der Aedoeagus-Tasche, of aedeagal pouch). *Basalchitinisierung* (Wagner, 1940), *keel* (Traub, 1950).
Caps	Capsula. *pumping bulb* (Sharif, 1945).
Cing	Cingulum (der Aedoeagus-Tasche, of aedeagal pouch) *girdle* (Traub, 1950).

Cing'	Distale Verlängerung des Cingulums, distal elongation of cingulum. *laterale Chitinrippe* (Wagner, 1940).
Cl	Clasper (Rothschild, 1902). *clasping apparatus, crochets génitaux* (Séguy, 1951). *Gonopode* (Wagner, 1939), *Haftapparat* (Landois, 1866). *parameres* (Snodgrass, 1946 ; Traub, 1950 ; Barrera, 1953).
Coll	Collum (des Aedoeagus-Apodems, of aedeagal apodeme) *neck of apodemal strut* (Traub, 1950).
Corp Cl	Körper des Claspers (Dampf, 1910), corpus (body) of clasper. *basimere, forceps* (Séguy, 1951).
dA	Dorsalarm (des Tubus interior), dorsal arm (of inner tube). *hook-like dorsal process* (Shariff, 1945) ; wenn distal verlängert : *semi-detached rod* (Hopkins & M. Rothschild, 1953), *apical process, dagger-like process.*
Db	Ductus bursae (Snodgrass, 1946). *Ductus bursae copulatricis* (Oudemans, 1909).
Dc	Ductus communis. *Ductus seminalis communis* (Snodgrass, 1946). *Pars communis* (Dampf, 1912).
Dej	Ductus ejaculatorius, ejaculatory duct.
di A	Distalarm (des St IX), distal arm (of St IX). *apical, horizontal, median arm.*
D obt	Ductus obturatus (Snodgrass, 1946). *Ductus obturatorius* (Lass, 1905).
dP	Processus dorsalis, Dorsalprozess (des Clasper-Körpers), dorsal process. *fixed process, immovable finger,* P^1 (Hopkins & M. Rothschild 1953), *unbeweglicher Finger/Fortsatz* ; wenn sekundär beweglich (in Pulicidae) : *clasper lobe* (Snodgrass), *Exopodit* (Wagner, 1939), *flap of clasper* (Jordan, N. C. Rothschild).
D sp	Ductus spermathecae, spermathecal duct. *Ductus receptaculi seminis* (Lass, 1905), *Ductus seminalis* (Dampf, 1910).
Dupl vag	Duplicatura vaginalis (Lass, 1905).
Endotd	Endotendons (des Endophallus, of endophallus). *Apophysen des Penis, copulatory rods* (Sharif, 1945), *levers of penis, penis rods* (Snodgrass, Traub), *springs of penis.*
Enph	Endophallus. *Penisfutteral* (Ioff, 1936), *phallotheca* (Sharif, 1945).
enph S	Endophallus-Sack, endophallic sack.
Epitd	Epitendon (des Aedoeagus-Apodems, of aedeagal apodeme).
F	Finger, finger (Rothschild 1898) (des Clasper-Körpers, of corpus of clasper). *Beweglicher Finger/Fortsatz, digitoid appendage/process, distimere, Endopodit* (Wagner, 1939 ; Ioff, 1936), *forcipule* (Séguy, 1951), *Gonopode* (Beier 1937), *harpago* (Barrera, 1953), *movable finger/process.*
F^1	oberer Finger, upper finger. *anterior process* (Hubbard, 1947), *F* (Holland, 1949), F' (Snodgrass), P^2 (Hopkins & M. Rothschild, 1953), Pr^2 (Dampf, 1910).
F^2	unterer Finger, lower finger. *Exopodit, F* (Snodgrass), F^1 (Holland, 1949), P^3 (Hopkins & M. Rothschild), *posterior process* (Hubbard), *Pr* (Dampf).

Fib vag	Fibula vaginalis (Lass, 1905).
Fist	Fistula (des Tubus interior, of inner tube). *Tubus exterior, outer tube.*
Fu	Fulcrum (des Aedoeagus-Apodems, of aedeagal apodeme). *apodemal strut* (Snodgrass, Traub), *condyli* (Jordan, 1939), *fulcral strut* (Snodgrass, Traub).
GC	Genitalkammer, genital chamber (Snodgrass). *end chamber* (Sharif), *Vagina* (Lass, 1905), *vestibulum vaginae* (Dampf, 1910).
Gl vag	Glandula vaginalis (Lass, 1905).
Gp	Gonopore.
Gtr	Gonotreme. *Orificium vaginae, Vaginalspalte* (Lass, 1905), *Vulva.*
Ham	Hamulus (des Aedoeagus, of aedeagus). *crochet* (viele Autoren), *harpago* (Sharif), *Parameren, parameres* (viele Autoren).
—	Hilla (Smit, i litt.). *appendix, neck, tail of spermatheca.*
Hypotd	Hypotendon (des St IX, der Aedoeagus-Tasche oder des Aedoeagus, of St IX, of aedeagal pouch or of aedeagus). *aedeagal apodemal rod* (Traub), *apodeme of pons coxalis* (Sharif), *apodemal rod of endophallus* (Snodgrass), *Apophyse des ST IX, apophyses basales* (Séguy, 1951).
i Tub	Tubus interior (des Aedoeagus), inner tube (Snodgrass) *penis tube, posterior sclerotic tube* (Sharif).
L	Lobus (Lappen, Vorsprung), lobe.
Lam l	Laminae laterales (des Aedoeagus-Apodems, of aedeagal apodeme). *lateral plates, lateral ridges* (Sharif), *mantle of phallosome* (Jordan, 1939).
Lam m	Lamina media (des Aedoeagus-Apodems). *Achsenskelett* (Wagner, 1940), *median ridge* (Sharif) *middle plate, Scheidewand des Leitskeletts* (Wagner).
Ld	Lobus dorsalis.
L int	Lobus intersegmentalis. *Intersegmentallappen* (*-lobus*), *intersegmental lobe.*
Ll	Lobus lateralis. am Aedoeagus: *Lamelle* (Peus, 1950).
Lsm	Lobus submedius.
lun Scl	Lunarsklerit (des Aedoeagus), lunar sclerite. *crescent sclerite* (Traub), *dorsal sclerite of pumping bulb* (Sharif), *tectum* (Jordan 1941).
M	Manubrium (Wagner, 1898) (des Clasper-Körpers, of corpus of clasper). *manubrium*[2] (Jordan & Rothschild, 1906).
Memb	Membran, membrane (membr = membranös, membranous).
Ost b	Ostium bursae (copulatricis). *Begattungskanal.*
Ov	Ovidukt, oviduct.
—	Papilla (Smit). *appendix of tail of spermatheca, Chitinknöpfchen, terminal appendage, Terminalknopf.*
P	Processus, Prozess (des Clasper-Körpers), process (of corpus of clasper).
P dil	Pars dilatata (Oudemans 1909) (des Ductus spermathecae, of spermathecal duct).

Pen	Penis.
pr A	Proximalarm (des St IX), proximal arm (of St IX). *ascending, basal, vertical arm, Seitenzweig.*
R	Ruga (der Dorsalblase, of aedeagal dorsal wall).
sap Scl	Subapikalsklerit (des Laterallobus des Aedoeagus), subapical sclerite (of aedeagal lateral lobe). *Parameren* (Peus, 1950, Wagner, 1940, in *Ctenophthalmus*).
Scl	Sklerit, sclerite.
Sens	Sensillum (des Fingers, of finger), Sensille.
Sham	Subhamulus (des Aedoeagus, of aedeagus). *hammer-shaped sclerite* (Sharif), *pseudocrochet* (Traub).
Sp	Spermatheke, Spermatheca. *Receptaculum seminis.*
St	Sternum.
Strig	Strigillen, Strigillae. *ridges, rugae of spermatheca.*
T	Tergum.
t Ap	Tergal-Apodem, tergal apodeme (Snodgrass). *Dorsalplatte, manubrium*[1] (Jordan & Rothschild 1906), *manubrium dorsale, upper manubrium.*
t Marg	Terminalrand (der Spermatheke,) terminal margin (of spermatheca).
Vag	Vagina. *Uterus* (ihr unterster Teil).
Vel	Velum (der Dorsalwand des Aedoeagus, of aedeagal dorsal wall). *Basalbuckel* (Wagner, 1940), *dorsal arched middle plate of aedeagal apodeme* (Traub), *sail* (Traub).
Ves	Vesicula, vesicle (des Tubus interior, of inner tube). *stalk of leaf-shaped ventral sclerite* (Sharif).
Vi	Virga (des Endophallus, of endophallus). *intramural rod* (Snodgrass, Traub).
Vid	Virga dorsalis.
Viv	Virga ventralis. *leaf-shaped ventral sclerite* (Sharif).
vP	Processus ventralis, Ventralprozess (des Clasper-Körpers), ventral process (of corpus of clasper). P^3 (Jordan & Rothschild, 1908), *spur* (Jordan, 1939).
WO	Wagner'sches Organ. *Organ X* (Wagner, 1932).

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NOTES AND DESCRIPTIONS OF COSSIDAE FROM NEW GUINEA (LEPIDOPTERA : HETEROCERA).

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With Two Plates.

This account is based chiefly on material from the following sources :

(1) The Third Archbold Expedition, communicated by the Museum Zoologicum, Bogor, Indonesia.

(2) The Carnegie Museum, Pittsburgh, U.S.A.

(3) Rijksmuseum van Natuurlijke Historie, Leiden.

(4) Zoological Museum, Amsterdam.

(5) Musée Royal Zoologique de Belgique, Brussels.

(6) Zoologische Staatssammlung, München.

(7) The private collection of Mr. R. Straatman, deposited in the Leiden Museum.

(8) The Entomological Collection of the Agricultural University, Wageningen.

Several private persons placed material at my disposal. I am especially indebted to Prof. Dr. M. Hering, of Berlin, for the loan of several type specimens. My sincerest thanks are due to all those who rendered valuable assistance.

A comprehensive review of the entire Malayan Cossid fauna is in preparation and may appear within a reasonable time. It will contain many taxonomic, morphological, bibliographical and other details which, for reasons of space, are omitted from the present paper. This account does not aim at giving a complete list, but treats a limited number of species only. Such an attempt would be rather premature, as the New Guinea fauna is probably very rich in Cossids of which our knowledge is still very poor.

The material in the Pittsburgh Museum was for the most part collected by Mr. W. Stüber near Hollandia, Humboldt Bay, North Coast. Several specimens from Fak-Fak, South Coast, Western New Guinea, collected by Mr. Pratt, are included. The Archbold Expedition was accompanied by a well known and experienced entomologist, the late Dr. L. Toxopeus, who collected in the neighbourhood of Hollandia (Prince Bernhard Camp) and also acquired several specimens from Mr. Stüber. Only a few specimens were captured in the interior of the island. Holo- and allotypes of the Archbold Expedition are intended for incorporation in the Leiden Museum.

A. *ZEUZERA* Latreille, 1804.

1. *Zeuzera indica* Herrich-Schaeffer, 1854.

The largest *Zeuzera*, easily recognisable, it ranges from the S.E. Himalayas, through the Archipelago to the Phillipines, New Guinea and North Australia, without forming marked subspecies.

1 ♂, Pr. Bernhard Camp (*Archbold Expedition*). 1 ♂, Mamberano River, (*Dr. Docters van Leeuwen*). Museum Bogor.

2. *Zeuzera coffeae reticulata* Joicey and Talbot, 1916.

Joicey and Talbot's diagnosis of *reticulata* is very short and quite inadequate. I have seen the type specimen in the British Museum and I have a small series of specimens from different localities in New Guinea which I ascribe to *reticulata*.

Colour of antennae varies from greyish-brown to black, pattern of thorax and abdomen, consisting of small, somewhat reduced dark bluish spots, inconspicuous. Markings of the fore wing formed by small interneural striae of a greyish colour ; in the hind wing these striae are obtuse or wanting.

Male genitalia (examined in several specimens) : Structure rather delicate, shape of valva slightly variable, lower ends of tegumen distinctly thickened just above articulation of valva, giving a somewhat elbowed appearance to this part of tegumen. Aedeagus small and rather weak, curved, not bulbous, without internal or vesical structure.

Female : Unknown.

2 ♂, Pr. Bernhard Camp ; 1 ♂, Araucaria Camp, 800 m. ; 1 ♂, Idenburg River, 35–48 mm. (*Archbold Expedition.*)

As already stated by Joicey and Talbot, the species comes very near to *coffeae* Nietner. It is certainly only a " weak " subspecies of *coffeae*, the male genitalia of both having the same characteristics. The correct name, therefore, is *Z. coffeae reticulata* Joicey and Talbot. *Zeuzera burgersi* Gaede, 1933, from the former German New Guinea, is a small specimen of *reticulata* only. I examined the genitalia of the holotype of *burgersi*, and they agree with those of *coffeae* and *reticulata*. The name *burgersi*, therefore, sinks as a synonym.

3. *Zeuzera roricyanea* Walker, 1861.

The late Dr. Toxopeus recognised and redescribed this species, which had been confused with *coffeae* by previous authors. Yet the male is easily recognisable by the colour of the antennal pectinations, which are distinctly fuscous. Furthermore, the interneural striation on both wings is obsolete or wanting, but a number of clear, small, dark spots are situated on the veins in the fore wing. The termen of the hind wing is not emarginate.

The species was described from Borneo. I have seen specimens from Indochina, Malaya, Sumatra, Java, Borneo, Celebes, Obi Major and the Philippines. From New Guinea it is recorded here for the first time.

Male genitalia (examined in specimens from Sumatra, Java and New Guinea) : Uncus rather short, valva elongate, about twice as long as broad ; in Sumatran specimens slightly pointed, in Javanese specimens rounded. Aedeagus short and thick, strongly curved, with its base bulbous, its apex pointed, without distinct internal or vesical structures.

1 ♂, 43 mm., Pr. Bernhard Camp. *Archbold Expedition* ; 1 ♂, about 42 mm., Hollandia, *Carnegie Museum.*

Z. neuropunctata Gaede, 1933, from S.E. Borneo, is merely a synonym, as already stated by Dr. Toxopeus.

4. *Zeuzera caudata* Joicey and Talbot, 1916.

Described from the Wandammen Mts., Dutch N. Guinea.

Easily recognisable by the shape of hind wing, which has the termen distinctly emarginate, before anal angle. Interneural markings, chiefly in fore wing, consist of many spots, not striae. Antennae greyish-brown to blackish. Thorax upperside dotted, not striped.

I examined the holotype and a number of additional specimens in the British Museum and at Tring, from Humboldt Bay, Brit. N. Guinea, New Ireland, Goodenough Island, the Solomons and Central Buru. 1 ♂, Finschhafen, former German New Guinea. In Mus. Munich.

Male genitalia : More robust than in the two preceding species. The lora, as I name the basal appendages of the tegumen, represent an incomplete gnathos, rather large and conspicuous ; they are weak in the *coffeae* group. Lower parts of tegumen straight, not elbowed as in *coffeae*. Aedeagus short and stout, straight, with a very strong internal and vesical structure that occupies more than half its length. A similar structure occurs in many *Xyleutes* males.

Female : Unknown.

Z. rhabdota Jordan, 1932, from Atjeh, Sumatra, agrees closely with *caudata* also in the male genitalia, but it has the thorax upperside striped, not dotted. It may be a distinct subspecies and should bear the name *Z. caudata rhabdota* Jordan (**stat. nov.**). I have seen many additional males in various Museums, and one female in the Paris Museum, from Sumatra. I hope to have the opportunity to describe them in more detail later.

B. *XYLEUTES* Hübner, 1822.

This generic name, evidently derived from the Greek xylon (= wood), must be considered as an anagram. As the type species is *crassa* Drury, and Hübner uses the plural " *Xyleutae* ", I treat it as feminine.

The genus has a circum-tropical distribution, the majority of the species are Australian. A. J. Turner (1945, *Proc. roy. Soc. Qd.* **56** (1944) : 49–63) published a " revision " of the Australian species ; unfortunately he omitted about two dozen species described by previous authors and even by himself!

5. *Xyleutes strix bubo* Butler, 1882.

A common species with a wide range, from N. India to the Philippines and New Guinea, forming weak subspecies. The specimens from New Guinea belong to the dark form described by Butler as *bubo* from New Britain. I have many specimens from N. Guinea and the N.-W. Moluccas.

Archbold Expedition : 14 ♂, 12 of them from Hollandia, one from Araucaria Camp, 300 m., and one from Rotan Camp, 1200 m.

6. *Xyleutes leucolopha* Guérin [1838].

This is the oldest name for a rather common species generally known as *leuconota* Walker, 1856, or *persona* Le Guill., 1841. Though the correct date of Guérin's description is not quite certain, there can be hardly any doubt that this name has priority. As a habitat Guérin gives " Amboina or New Guinea "; I think it would be advisable to fix New Guinea as the topotypical locality.

Turner (*loc. cit.* : 58) has described a *Xyleutes leucolopha* from Australia. I propose to replace this homonym by *turneri* **nom. nov.**

This species has the same wide distribution as the preceding one, viz. from N. India to New Guinea, forming no marked subspecies, though the general pattern in the Papuan specimens is more vivid and, therefore, more contrasting than in specimens of a more western origin.

Archbold Expedition : 6 ♂, 87–158 mm., 4 of them Pr. Bernhard Camp, 2 Ampas.

7. *Xyleutes ceramica* Walker, 1865.

A common species with a wide range from Burma and Indochina through the Archipelago and N. Guinea. No subspecies are distinguishable. *X. bosschae* Heylaerts, 1892, from Borneo is merely a synonym.

Carnegie Museum : 13 ♂ and 1 ♀, Hollandia and surroundings ; 1 ♂, Fak-Fak.

Archbold Expedition : 3 ♂, Pr. Bernhard Camp.

Straatman collection : 1 ♂, 82 mm., Gamadodo, Milne Bay.

8. *Xyleutes mineus* **pallescens** subsp. n.

The collective species occurs from N. India through the Archipelago, reaching the Philippines and New Guinea.

Generally less common than preceding species and easily recognisable by its obvious pattern. In Amboina (and neighbouring islands?) a subspecies *hyphinoe* Cramer, 1777, occurs with much enlarged and confluent dark markings. In New Guinea specimens the ground colour much paler, about pale dirty-yellowish, as already observed by Gaede (1932, *in* Seitz *Grossschmett. Erde*, **10** : 818), but this author ascribes it erroneously to fading. A tendency to have the dark patches enlarged as in *hyphinoe* or even more. In extreme cases the pale ground colour has almost completely disappeared, leaving only a discal pale streak in the fore wing. This very dark form deserves a name : *Xyleutes mineus pallescens* forma **archboldi** f. n. (Plate I, fig. 1).

Female : No females from New Guinea are known to me.

Archbold Expedition : 5 ♂, Hollandia and Pr. Bernhard Camp, with holotype of *pallescens* and *archboldi* and 4 transitional forms.

Carnegie Museum : 8 ♂, Hollandia and surroundings, including one transitional specimen to f. *archboldi*.

9. **Xyleutes cinerosa** sp. n. (Plate I, fig. 2.)

Male : Palpi dark brown, head white, antennae light greyish-brown. Patagia and tegulae white, mesonotum light greyish-brown. Fore wing whitish, with the usual greyish-brown reticulation. Two dark spots along costa only, more or less vaguely indicated, a small brown spot on vein 1*a*–*b*, a narrow space bordering it at inner side, more pure white. Hind wings greyish with a slightly darker and denser reticulation. Abdomen covered with white and brownish scales. Underside about the same as upperside, the costal spots on fore wing less marked, the interneural reticulation in terminal area more condensed in brown dashes. Legs whitish, the tarsi with brown bands.

Male genitalia (Plate II, fig. 1) : Large and robust, of the usual shape. Aedeagus short and stout, slightly bent, apical part bulb shaped, having a striate appearance due to many dense folds in its interior. Juxta inconspicuous, but with two long pointed appendages, situated on each side of aedeagus. I call these appendages, which are typical in *Xyleutes*, " ligulae ".

Female : Similar to the male, but generally darker, the reticulation more fused into patches, chiefly between the veins in fore wing. Basal half of antenna distinctly bipectinate, branches, however, not so long as in male.

Archbold Expedition : Holotype ♂, 95 mm., Humboldt Bay ; Mt. Haga. Paratypes, 2 ♂, 93 and 97 mm., Slager resp. Ampas.

Museum Bogor : 1 ♀, 85 mm., Motorbivak, viii.1926 (*Docters van Leeuwen*) ; 2 ♀, 63 and 80 mm., Ampas, one of them allotype.

10. **Xyleutes jordani** sp. n. (Plate I, fig. 9.)

Male: Similar to the preceding, but the entire ground colour more pure white, the reticulation less dense, more striate. The costal patches small and narrow, brown, the spot on vein 1*a*–*b* reduced to a small point. Body, underside and legs whitish, the latter with a rusty pilosity. Palpi and antennae light brownish.

Male genitalia (Plate II, fig. 2) : Rather strong, but markedly smaller and shorter than in *cinerosa.* Uncus shorter, upper margin of valva more emarginate, saccus shorter and broader, aedeagus less curved, oral part very bulbous, its foldings very intricate.

Archbold Expedition : Holotype ♂, about 82 mm. (both apices in fore wing damaged), Cyclops Mts., about 900 m.

11. **Xyleutes papuana** sp. n. (Plate I, fig. 8.)

Male : Ground colour in fore wing whitish, with the usual greyish-brown reticulation. No basal patch. Costa with an elongate dark brown patch near base, rather well marked, and a second patch nearer to apex, of an irregular shape or somewhat triangular. Some specimens with a darker shade or dash along inner margin. Hind wing light dirty-greyish, the reticulation weak. Cilia in both wings alternately greyish and white. Underside variable, more or less diffuse or with a rather clear brown reticulation on a white background.

Head, antennae and patagia dark brown, tegulae greyish-white, dorsum of mesonotum more or less brownish. Abdomen rather light greyish, the legs more or less variegated with dark brown.

One of the males from Pr. Bernhard Camp is smaller, measuring 57 mm., and obviously darker with the tegulae greyish-brown.

Male genitalia (Plate II, fig. 3) : Much smaller and less robust than in *cinerosa,* upper margin of valva in basal part emarginate, aedeagus less stout, bulbous, with the inner foldings less prominent. Juxta with the ligulae shorter, the latter more ear shaped.

Female : Similar to the male, the general coloration somewhat lighter.

Carnegie Museum : 14 ♂, 43–60 mm., Hollandia ; 1 ♀ (allotype), Fak-Fak (*Pratt*), badly damaged.

Archbold Expedition : 2 ♂, Pr. Bernhard Camp, and 2 ♂, Ampas, including holotype, 60–62 mm.

Straatman collection : 1 ♂, Biak, dwarfed and right fore wing badly damaged.

The species resembles *X. cinerosa,* but is smaller and somewhat darker. The patagia are brown, the costal patches in fore wing more prominent, the patch along inner margin more dash like.

12. *Xyleutes tectoria* Swinhoe, 1901.

The identity of this species has been confirmed by examination of the type in the British Museum. It was described from one male from the Solomons ; a redescription is advisable.

Male : Antennae and palpi dark brown, head, thorax and abdomen light purplish-brown, mesothorax with two longitudinal dark brown stripes. Fore wing white, with the basal area sharply bordered, dark purplish-brown. Costa with two dark patches, the outer one, as well as the patch along vein 1*a*–*b*, small. Reticulation moderately dense, blackish or purplish-brown, somewhat confluent in the interneural spaces near termen. Hind wing darker, the reticulation dense. Underside more contrasting. Legs dark brown, tarsi with white bands.

Male genitalia (Plate II, fig. 4): Of the usual shape. Aedeagus less stout, slightly bent, slightly bulbous, the striation in its interior distinct.

Female: Unknown.

Archbold Expedition: 1 ♂, 79 mm., Ampas; 2 ♂, Ampas, 70–76 mm.; 1 ♂, 46 mm., dwarfed, Pr. Bernhard Camp.
Carnegie Museum: 4 ♂, Hollandia.
Straatman collection: 1 ♂, 72 mm., Biak.

The species is easily recognisable by its purplish-brown tinge and the large basal patch on the fore wing.

13. **Xyleutes elegans** sp. n. (Plate I, fig. 4.)

Male: Head with palpi and antennae, patagia and mesonotum dark chocolate-brown. Tegulae white. Abdomen light chocolate-brown, intermingled with many white scales. Fore wing white, with two large, deep chocolate-brown costal patches, the basal one somewhat extending into midcell, but not reaching hind margin. The patch on vein 1*a*–*b* very small. The reticulation rather delicate and regular, brownish.

Male genitalia (Plate II, fig. 5): Of the common type. Uncus slightly thickened, chiefly when seen from above. Upper margin of valva slightly sinuate. Aedeagus moderately strong, only bent at base, slightly bulbous, with its interior striation distinct. Juxta with the ligulae small, not obvious.

Female: Unknown.

Archbold Expedition: 2 ♂, 47–54 mm., Mist Camp and Mook Camp, both 1800 m., the latter holotype.

14. **Xyleutes albicans** sp. n. (Plate I, fig. 5.)

Male: A small species. Palpi brown, antennae greyish-brown, head, thorax and abdomen white, intermingled with brown scales. Fore wing white with the greyish reticulation rather faint, costal patches less prominent, small and narrow, greyish-brown. In the holotype the dark spot on vein 1*a*–*b* is small and narrow, in the paratype wanting. Hind wing light greyish, with a weak, grey reticulation. Underside of wings whitish, with the light brown reticulation more dominating. Legs whitish, tibiae and tarsi more or less brown, the latter banded.

Male genitalia (Plate II, fig. 6): Correspondingly small, but of the usual type. Upper margin of valva sinuate, somewhat excavate in basal part. Aedeagus less stout, slightly bent, slightly bulbous, its interior striate. Juxta inconspicuous, the ligulae of normal shape and size.

Female: Unknown.

Carnegie Museum: 1 ♂ (Paratype), about 35 mm., Hollandia.
Straatman collection: 1 ♂ (holotype), 43 mm., Biak.

15. **Xyleutes perdrix** sp. n. (Plate I, fig. 6.)

Male: Body, including head, palpi and antennae whitish, intermingled with many greyish-brown scales. Both wings white, with a rather dense and regular, obvious dark grey reticulation. No costal patches, no patch on vein 1*a*–*b*, but in anal area the reticulation in some specimens more or less confluent, causing a darker coloration of this area. Cilia alternately grey and white. Legs white, the tarsi grey with white bands.

Male genitalia (Plate II, fig. 7): Valvae rather broad and short, upper margin nearly straight. Aedeagus short, rather straight, less bulbous, the interior striation weaker than in other species.

Female: Resembling the male, but the reticulation less dense and less prominent, general coloration, therefore, lighter.

Archbold Expedition: 1 ♂ (holotype), 47 mm., Ampas; 4 ♂, 41–52 mm., Mt. Haga, Araucaria Camp, 800 m. and Bewari River Territory.

Carnegie Museum: 3 ♂ (paratypes), 1 ♀ (allotype), Ninay Valley, Arfak Mts., Dutch New Guinea.

C. *DUDGEONEA* Hampson, 1900.

A very remarkable genus, based on the species *leucosticta* Hampson from the Eastern Himalayas. Hampson mentions a form from Sierra Leone, W. Africa, which was afterwards named by Strand as *sierraleonensis*. Gaede (1929, *in* Seitz, *Grossschmett. Erde* **14** : 544) records it from Transvaal. Mabille, 1879, has described a species from Madagascar, as *Endagria locuples*, which was placed by Dalla Torre, 1923, in *Dyspessa* and by Gaede, 1929 correctly in *Dudgeonea*. I have seen three males in the Leiden Museum from Madagascar which perhaps belong to a new species. In 1902 Turner described another species as *Dudgeona* (sic!)) *actinias*, from Townsville, Queensland, N. Australia. In 1945 he added a fifth one, as *lichnocycla*[1] from Carnarvon Range, Queensland, without mentioning *actinias*. Judging from the descriptions, both species may be different. Regarding the life history of *actinias* he cites Mr. F. P. Dodd, " who states that the larvae have the habits of *Xyleutes*. Like that genus, the pupa has to break through a thin covering of bark, and then protrudes while the moth emerges ".

It is interesting that in Northern New Guinea a species occurs of which the Carnegie Museum sent two males, both from Hollandia. I think they represent a new species.

16. **Dudgeonea nummata** sp. n. (Plate I, fig. 7.)

Male: Palpi well developed, with a rather long second segment. Third segment about one-third second, rather blunt. Proboscis rudimentary. Antennae in both specimens unfortunately missing, but one of them has the basal part of the right antenna preserved. Here the segments are very short and thickened, not bipectinate as in the species hitherto described. Venation in both wings about the same as in the type species, complete, all veins free, vein 11 from about three-fifths of the upper margin of cell. In hind wing vein 6 and 7 originate from the same base, at upper angle of cell. Frenulum obviously long and strong, nearly half costa of hind wing. Hind tibiae with two pairs of uneven spurs. Underside of tarsal segments with about three spines each; claws with arolium well developed, of normal structure.

Differs from *leucosticta* and *lichnocycla* by its larger size, the straight costa in fore wing and probably by the very different male antenna. Ground colour of fore wing is a vivid chestnut-brown, darker in one specimen than in the other; hind wing lighter brown. Fore wing with many circular patches of a light yellowish (greasiness?) or silvery-white coloration, arranged in apical part, along costa and near base. On each tegula an obvious white patch.

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[1] Turner writes " *lychnocyla* ", but gives the derivation from the Greek " *lichnocyclos* " so that a printing error or an error in transcription is evident. The correction, therefore, is justified.

Male genitalia (Plate II, fig. 8): Typically cossoid, coming nearer to *Zeuzera* and *Xyleutes* than to *Cossus* and other genera. Uncus slightly bent and beak-shaped. Lora very distinct and long, reaching about middle of valve. Valva short and broad, rounded, juxta present, without appendages, saccus somewhat longer than in other Cossids. Aedeagus obviously long and slender, its basal part tapering, its orifice with the bladder-like vesica extruded, without special structures.

Female: Unknown.

Carnegie Museum: 2 ♂, 40 mm., holo- and paratype.

In view of its geographical distribution—W. and S. Africa, Madagascar, E. Himalayas, N. New Guinea and N. Australia—the genus *Dudgeonea* must be of old origin. Moreover, the described species display a great similarity in their general features, very different from that of all other Cossids known, but the male genitalia leave no doubt that these insects are true Cossids ranging near *Xyleutes*. The structure of the male antenna in the new *D. nummata*, as far as can be judged from the defective material, makes it perhaps advisable to place this species in a new genus or at least in a new subgenus.

PLATE I.

Fig. 1.—*Xyleutes mineus pallescens* form *archboldi* f. n. ♂.
Fig. 2.—*X. cinerosa* sp. n. ♂.
Fig. 3.—*X. tectoria* Swinhoe ♂.
Fig. 4.—*X. elegans* sp. n. ♂.
Fig. 5.—*X. albicans* sp. n. ♂.
Fig. 6.—*X. perdrix* sp. n. ♂.
Fig. 7.—*Dudgeonea nummata* sp. n. ♂.
Fig. 8.—*Xyleutes papuana* sp. n. ♂.
Fig. 9.—*X. jordani* sp. n. ♂.

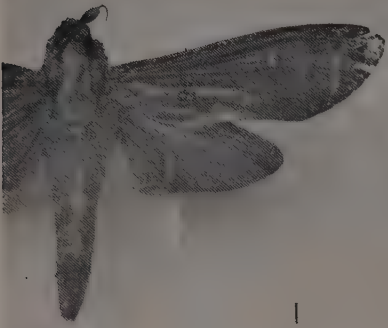
(About natural size; Photogr. W. Roepke.)

PLATE II.

Male genitalia.

Fig. 1.—*Xyleutes cinerosa* sp. n.
Fig. 2.—*X. jordani* sp. n.
Fig. 3.—*X. papuana* sp. n.
Fig. 4.—*X. tectoria* Swinhoe.
Fig. 5.—*X. elegans* sp. n.
Fig. 6.—*X. albicans* sp. n.
Fig. 7.—*X. perdrix* sp. n.
Fig. 8.—*Dudgeonea nummata* sp. n.

(About 7·5 × natural size; Microphotogr. Botanical Laboratory, Wageningen.)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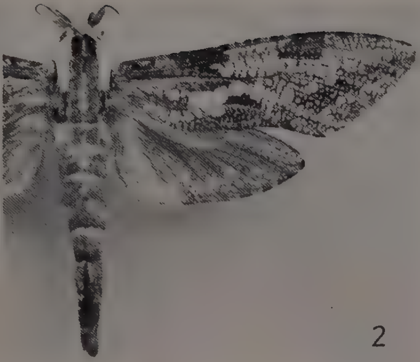
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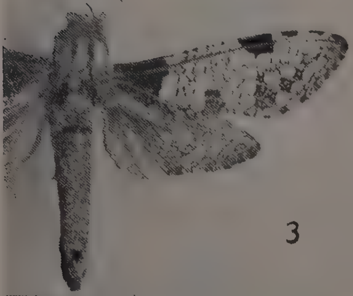
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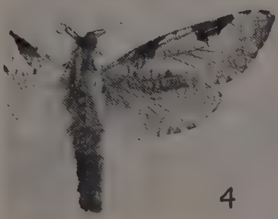
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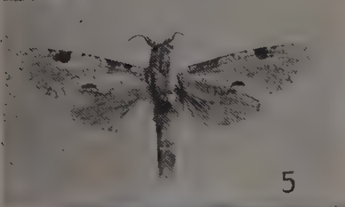
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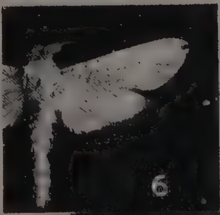
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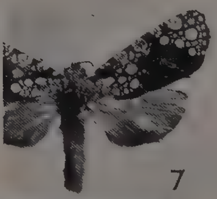
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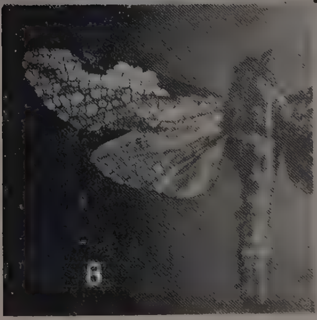
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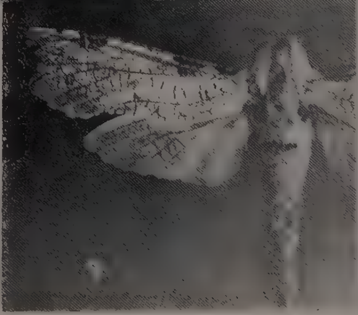
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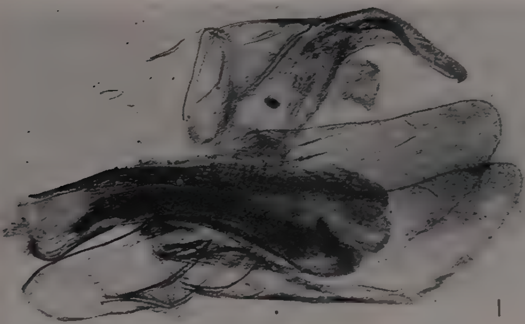
Notes and descriptions of Cossidæ from New Guinea.

W. Roepke. *Adlard & Son, Ltd., Dorking*



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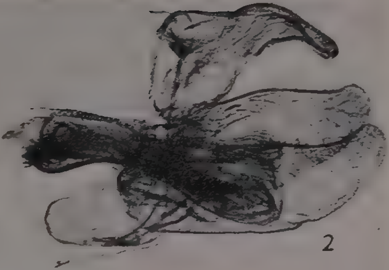

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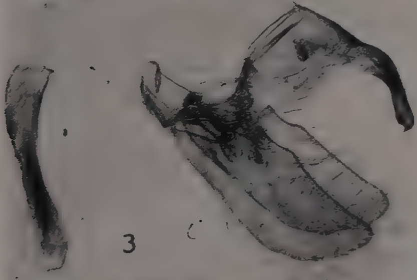

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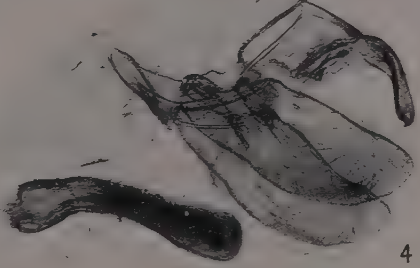

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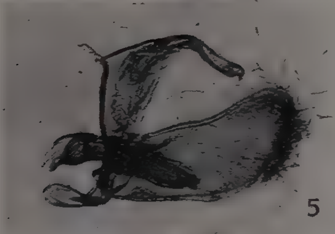

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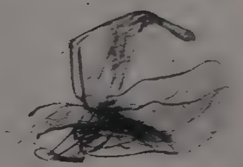

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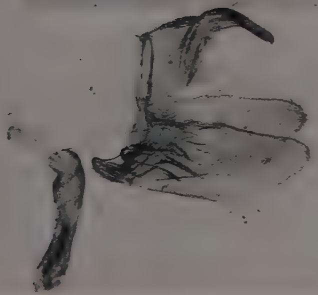

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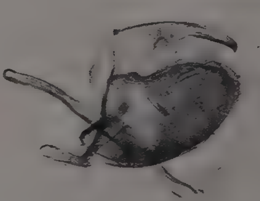

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Notes and descriptions of Cossidæ from New Guinea.

W. Roepke.

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THE SPERMATOZOA OF THE HONEY-BEE.

By Lord Rothschild.
(*Department of Zoology, University of Cambridge.*)

With 2 Plates and 4 Text-figures.

The original purpose of this paper was to record some new observations on the morphology of honey-bee spermatozoa. But when I started to make these observations, on spermatozoa obtained from the spermatheca of a queen, it was natural to ask how they remain alive for so long in the spermatheca, and how they get into it. As regards the first question, spermatozoa which rely on the combustion of endogenous substrates for their energy requirements, such as those of the sea-urchin, have a comparatively limited life, of the order of days, even when their movements are restricted by close packing and lack of oxygen. When substrates are available in the external medium, as in the case of mammalian spermatozoa in their normal medium, seminal plasma, the life of the spermatozoon is again of the order of days, unless the temperature is reduced to "non-physiological" levels. According to Berrill (1954), the longevity of bat spermatozoa, which are said to remain alive and be able to fertilise eggs after five or six months in the uterus of the female, is due to the temperature of the female bat falling in the winter to within a few degrees of the external temperature, 1–5° C. No information is available as to how bee spermatozoa remain alive, for years, in the spermatheca of the queen; they probably obtain nutrient substances from secretions of the spermatheca or appendicular glands, and do not rely exclusively on endogenous substrates. Alternatively, the secretions of the appendicular glands may exert an inhibitory effect on their activity and metabolism, a possibility which could be tested experimentally without much difficulty.

As regards the second question, how do the spermatozoa get into the spermatheca, it is surprising that, in spite of the number of observations which have been made on the sexual organs of the drone and the queen, there should still be no unanimity of opinion about the method by which the spermatozoa are injected into the queen. As certain of the more recent views on this subject are only to be found in obscure journals, it may be useful briefly to record some of them. They are mainly based on the statements of Bishop (1920), Herrod-Hempsall (1937) and Fyg (1952).

Copulation.

The principal parts of the male reproductive system are shown, diagrammatically, in fig. 1. At the moment of copulation, or when the drone is killed or anaesthetised in certain ways, part of the system turns inside out, or everts. The external appearance of the everted organs is shown in fig. 2, which is based on a drawing by Mackensen and Roberts (1948). The fimbriate lobe, whose function is unknown, has been omitted. The suggestion has sometimes been made that the genital organs would be more easily everted in flight than on the ground and that copulation therefore must take place in the air. Herrod-Hempsall (1937 : 1627) says, "To enable him to extrude his *penis*, it is

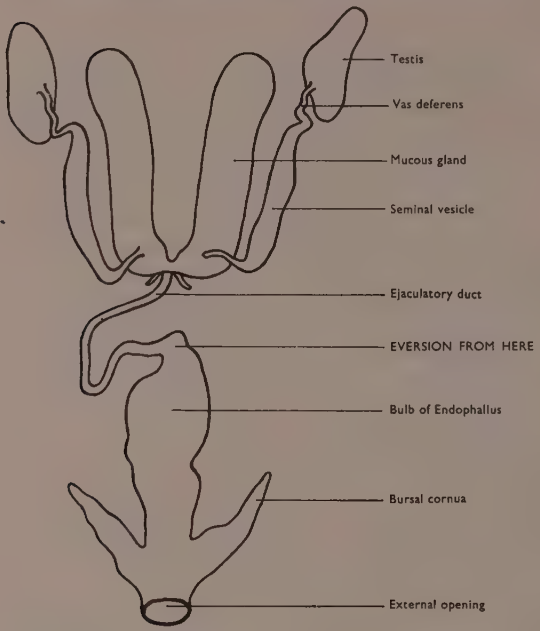
Testis
Vas deferens
Mucous gland
Seminal vesicle
Ejaculatory duct
EVERSION FROM HERE
Bulb of Endophallus
Bursal cornua
External opening

FIG. 1.—The male reproductive system of the honey-bee (simplified and diagrammatic).

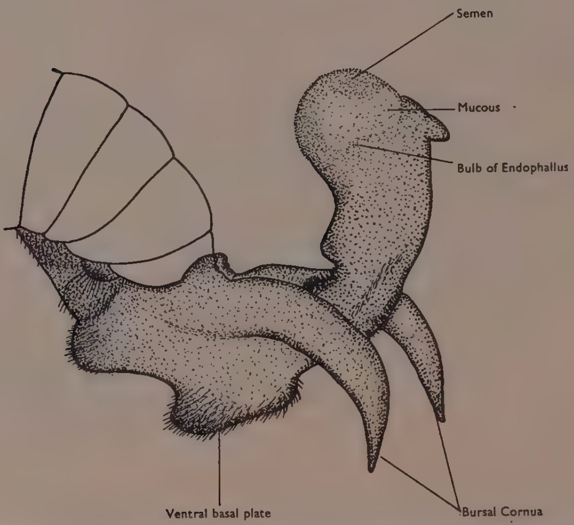
Semen
Mucous
Bulb of Endophallus
Ventral basal plate
Bursal Cornua

FIG. 2.—Male reproductive organs of the honey-bee, everted (*after* Mackensen and Roberts, 1948). Some structures have been omitted for the sake of simplicity.

absolutely essential that his air sacs be fully inflated, and his stomach full of food, for only then can he exert the muscular pressure on the abdomen which plays a part in forcing out the organ. This explains why coition takes place on the wing, for it is then only that the drone's air sacs are filled to their utmost capacity, and his stomach completely loaded, because he rarely leaves home for a flight without having previously partaken of a good meal." Although copulation probably does take place in the air, under normal conditions, there is little evidence in favour of the view that eversion would be facilitated under these conditions. As is well known, anaesthesia may induce eversion, which does not support the contention that flight, fully distended air sacs and a full stomach are pre-requisites of copulation.

There has been much discussion about the positions of the drone and the queen during copulation. Consideration of fig. 2 shows that the most probable position is with the queen on top of the drone, as in fig. 3*a*, because, in the everted position, the external opening of the ejaculatory duct points slightly upwards and forward. In this position, however, the *bursal cornua* would not have any function. According to Herrod-Hempsall (1937), the drone is on top of the queen during copulation, but fig. 3*b* suggests that coition would not be possible in this position. Herrod-Hempsall's photograph of a drone and a queen during what he calls "the act of attachment" (p. 1627) is not incompatible with the queen having been on top of the drone during copulation, and the same applies to Newbury's report (1937). According to Bishop (1920), the drone and the queen copulate face to face. This position, fig. 3*c*, is more probable than the one suggested by Herrod-Hempsall, but perhaps less so than the one shown in fig. 3*a*. In spite of what has been said above, it is only right to mention that, when stating that the drone mounts on the back of the queen (1937 : 1627), Herrod-Hempsall says: "This is not a statement born of supposition, for the writer has seen the act on numerous occasions."

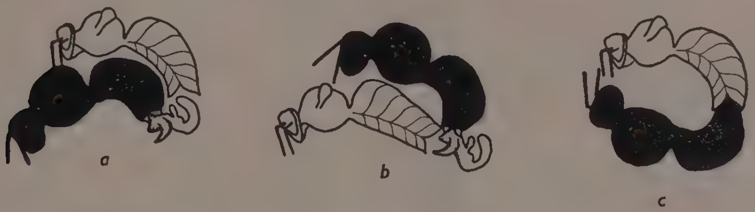

FIG. 3.—(*a*) Most probable position of drone and queen during copulation. (*b*) Position of drone and queen during copulation, according to Herrod-Hempsall (1937). Note the difficulties involved in this position. (*c*) Position of drone and queen during copulation, according to Bishop (1920).

The semen is deposited in the vagina and oviducts. There are differences of opinion about the time that the spermatozoa take to reach the spermatheca. According to Laidlaw (1944), the process only takes a few minutes; but the more usual view is that the spermatozoa enter the spermatheca about five-and-a-half hours after copulation. After the emission of semen, the mucous glands (fig. 1) discharge their contents, which coagulate or clot on contact with the air, forming a plug in the sting cavity of the queen. A similar copulatory plug or *bouchon vaginal* is found after coitus in many mammals, such as rats, hedgehogs, bats and marsupials. In mammals, coagulation is due to the action of an enzyme, vesiculase, which, in rodents, is secreted by the so-called " coagulating gland ", adjacent to the seminal vesicle (Mann, 1954).

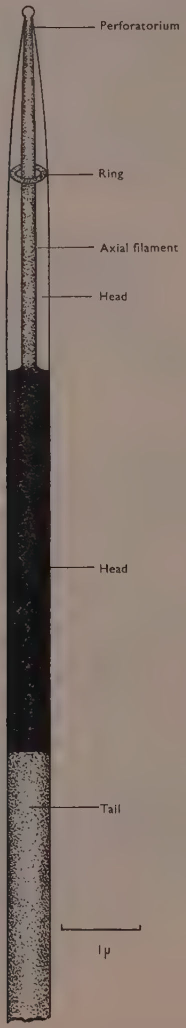

Fig. 4.—Anterior end of honey-bee spermatozoon, based on electron micrographs taken by Bretschneider (1950) and at Cambridge. In some specimens the anterior end of the head tapers more sharply than in the drawing.

MORPHOLOGY OF THE SPERMATOZOON.

The spermatozoon of the honey-bee is atypical in having a head and tail, but no middle-piece (fig. 4). The posterior half of the head is much more opaque to electrons than the anterior half, in which an axial filament, terminating in a "perforatorium", is clearly discernible. A ring-shaped structure, which may be homologous with the Ring Centriole situated at the posterior end of the middle-piece of a typical spermatozoon, can be seen in some, but not all, specimens, about 2μ below the tip of the "perforatorium".

Most spermatozoa have an obvious middle-piece between the head and the tail. Mitochondria-like structures are located in the middle-piece (Wilson, 1928), together, probably, with endogenous substrates (Rothschild and Cleland, 1952). Transverse sections of the tail of the honey-bee spermatozoon show the usual arrangement of fibrils, characteristic of all unicellular, vibratile protoplasmic structures in the animal and plant kingdom. This consists of nine fibrils, in a circular array, with two smaller fibrils in the centre (Plate I). The shapes of the nine outer fibrils, and their arrangement relative to each other such that the whole system resembles a catherine-wheel, have not been observed in any other spermatozoon. In addition, the tail of the honey-bee spermatozoon is unusual in containing two mitochondrial strands, apart from the usual eleven fibrils. These strands, which run along almost the whole length of the tail, exhibit cross striations. It is tempting and plausible to assume that they take the place of the conventional middle-piece and its mitochondria. They terminate about 7μ from the end of the tail which tapers at this point, possibly because the fibrils end one by one, at different distances along the tip of the tail, as in fern spermatozoa (Bradfield, 1953).

MOVEMENTS OF THE SPERMATOZOA.

Spermatozoa move by propagating S-shaped or, on occasions, helical waves along their tails. When they are packed closely together, their tail movements become synchronous. Intuitively, it may seem obvious that sperm tails will beat in phase when near to each other, because the tails will get in each other's way less when in, than out, of phase. But it was only in 1951 that Taylor showed, mathematically, that when the phase of the wave in one tail lags behind that in another, there is a strong reaction due to the viscous stress in the fluid between them, which tends to force the two wave trains into phase. If the ratio (distance between two vibrating sheets)/(wave-length of vibrations) is 1/10, the rate of energy dissipation when the waves are in phase is only one-thousandth of the rate when the waves are out of phase.

Bishop (1920) reported that bee spermatozoa vibrate in phase; but the phenomenon is so remarkable that it seems worth recording what the spermatozoa look like in these conditions (Plate II).

SUMMARY.

(1) Some new observations on the morphology of the honey-bee spermatozoon have been made.

(2) Problems associated with the positions of the drone and the queen during copulation are discussed.

ACKNOWLEDGMENTS.

I am indebted to Dr. J. R. G. Bradfield, the Cavendish Laboratory, University of Cambridge, for taking the electron micrographs reproduced in Plate I; to Dr. C. G. Butler, of the Bee Department, Rothamsted Experimental Station, for much advice and assistance, including the provision of spermathecae; and to Prof. V. B. Wigglesworth, F.R.S., for reading the manuscript of this paper.

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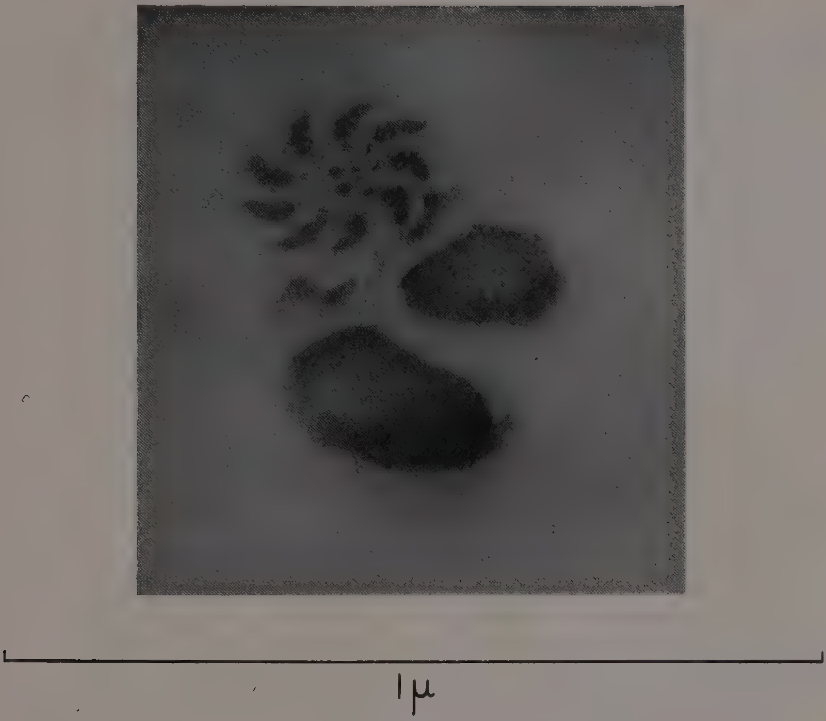
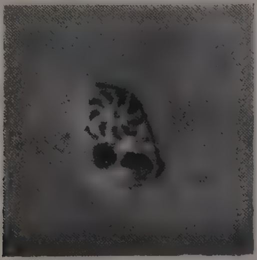


a.—Transverse sections of tail of honey-bee spermatozoon, × 120,000, showing nine fibrils arranged in a circular array and two smaller fibrils, diameter app. 120 ångstroms, in the middle. The two centre fibrils appear to be connected by a semicircular structure. There is, also, a suggestion that some of the nine outer fibrils are double and actually consist of two separate sub-fibrils. The two mitochondrial strands at 3.30 and 5.30 o'clock are normally enclosed, together with the fibrils, by the tail membrane, which has disintegrated. The structures between each of the mitochondrial strands and the array of fibrils are real; they have not been observed in other sperm tails.



b.—Transverse section of tail of honey-bee spermatozoon, × 32,000 with part of the tail membrane intact.

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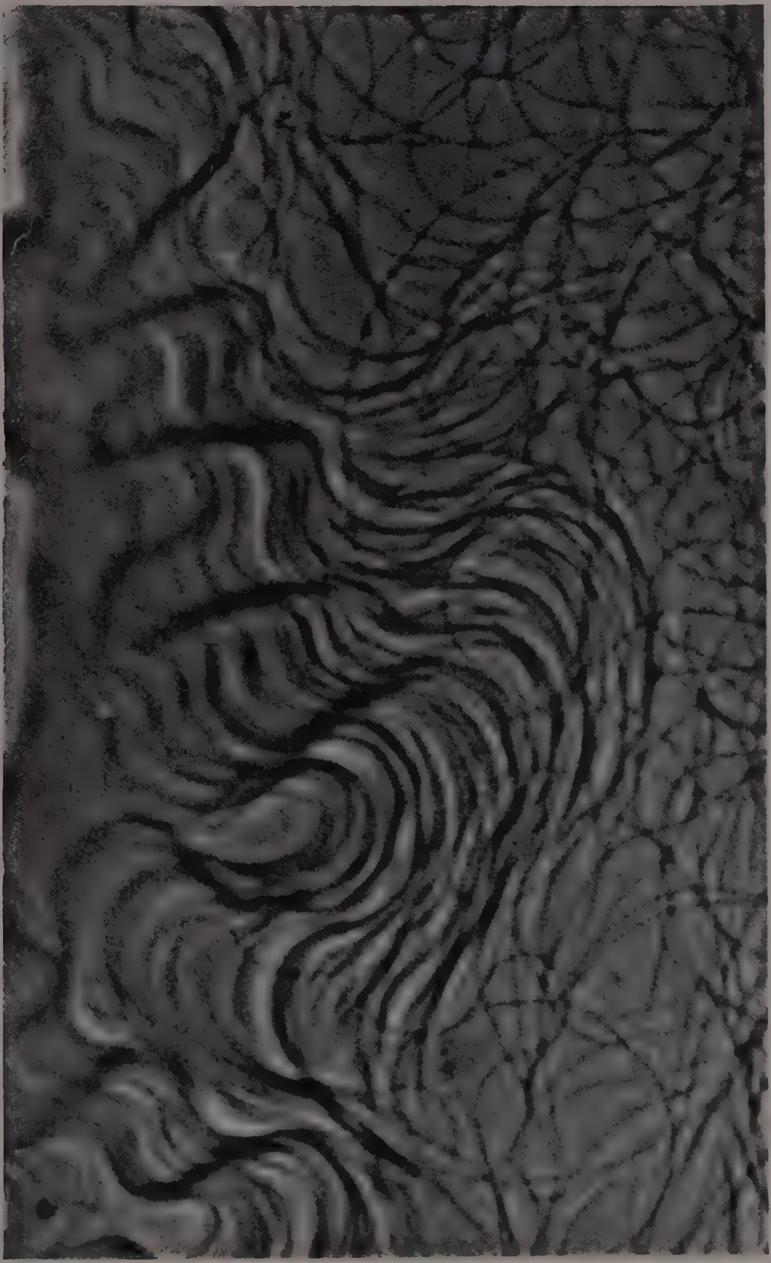

Spermatozoa of the honey-bee exhibiting synchronous movements. Exposure, 1/100th sec. Magnification, 790. C.T.S. phase contrast.

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THE DISTRIBUTION OF *CERATOPHYLLUS BOREALIS* ROTHSCHILD, 1906 AND *C. GAREI* ROTHSCHILD, 1902, WITH RECORDS OF SPECIMENS INTERMEDIATE BETWEEN THE TWO.

By Miriam Rothschild.

With 11 Text-figures.

Introduction.

In a previous paper (Rothschild, 1948) attention has been drawn to the curious distribution of *Ceratophyllus borealis* Rothschild. This species had up to that time been recorded from outlying islands round the north and west coasts of Great Britain and Ireland (Isle of St. Kilda (1), Shetland Isles (5), Inishtrahull (2), Scilly Isles (3)), from the Island of Ushant, France (8), Iceland (4), Finland[1] (several) and various localities in the Alps (5). There was a single record of a male *C. borealis* from the mainland of Britain. This specimen was found by G. B. Thompson, together with *C. garei* (both determined by the late Professor Julius Wagner) in the nest of a Wheatear (*Oenanthe oenanthe* (L.)), collected by C. L. Collenette at Parwich, Derbyshire. In addition there were three female specimens in the Waterston collection (British Museum) from the nest of the Dipper (*Cinclus cinclus* L.)[2] and Herring Gull (*Larus argentatus* Pontop.) from the mainland of Scotland, which appeared to be intermediate between *C. borealis* and *C. garei*. I had unfortunately missed three records in the literature to which F. G. A. M. Smit has since kindly drawn my attention. The first concerns a female in the Oudemans collection (Oudemans, 1915) from the nest of the Wheatear at Wassenaar on the coast of Holland. Originally determined by N. C. Rothschild, this specimen has recently been seen by Smit. Another specimen, collected at Leiden, formerly in the Oudemans collection, has been lost and therefore cannot be checked. The second record is from the Snow Bunting (*Plectrophenax nivalis* (L.)) at Utorkait, West Greenland (G. D. Hale Carpenter, 1938) collected by the Oxford University Expedition. This is a typical female which I have been able to examine, thanks to a loan from the University Museum, Oxford. The third record concerns a figure in Ioff (1936 : 121) of the spermatheca and the duct of the bursa, etc. The caption reads : " *C. borealis* (Kaukasus) ".[3] There are no details with regard to host or exact locality, but the spermatheca as shown is typical of the species. Since 1948 another record has been received from West Greenland, one male and one female of this species, collected by C. Vibè free on the ground at Korgut ; these were determined by F. G. A. M. Smit and seen by myself. Miss Theresa Clay has sent me the record of a male from the body of a Wheatear on Great Blasket Isle (south-west coast of Ireland), collected by S. M. D. Alexander and determined by F. G. A. M. Smit. Several specimens have been collected by myself from the nests of Snow Finches (*Montifringilla nivalis* (L.)) at Eigergletscher (2320 metres), Bernese Oberland, Switzerland. Specimens were collected from Wheatear's nests on Skokholm Island by P. J. Condor (G. B. Thompson, 1951, *Rep. Skokholm Bird Obs.* **1951** : 41–42), and a large and interesting series of records has been supplied by Kenneth Williamson from Fair Isle (*see below*). Typical *C. borealis* and intermediates between *C. borealis* and *C. garei* were obtained from nests of the following hosts on the mainland of Britain : Meadow Pipit (*Anthus pratensis* (L.)), Cross Gill, Cumberland, Grey Wagtail (*Motacilla cinerea* Tunst.), Ring Ousel (*Turdus torquatus* L.) and Wheatear from the Moorhouse Nature Reserve, Alston, Cumberland (nest and fleas collected by Mr. Coulson and Dr. Lewis Davies, fleas determined by the author and F. G. A. M. Smit), from the nests of the Whinchat (*Saxicola rubetra* (L.)) and Wheatear (3) at Laugharne Burrows, Carmarthenshire (nests collected by J. F. Thomas, fleas determined by the author and checked by F. G. A. M. Smit). An exhaustive re-examination by F. G. A. M. Smit of the material in alcohol in the Waterston (British Museum) collection has revealed two further specimens of *C. borealis* from the mainland of Scotland. Both are from nests of the Grey Wagtail (*Motacilla cinerea* Tunst.), one from near Loganlea Waterfall, Midlothian, and the other from Hillend, Midlothian ; both specimens are females, the former collected together with one female *C. garei* and three female *D. g. gallinulae*, the latter with two male and five female *D. g. gallinulae*. He also found a possible intermediate between *C. garei* and *C. borealis* (with more marked characteristics of the former) from the nest of *Columba livia* Gm. from Little Roe Island, Yell Sound, Shetland Isles. Another perfectly intermediate female was recently collected from the Fulmar Petrel (*Fulmarus glacialis* (L.)) from Caen Tar, Heisker, Outer Hebrides, by Ronald M. Allan.[4] In the Rothschild collection (British Museum) there are four specimens labelled

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[1] In the previous paper I suggested that the Finnish records (Nordberg, 1935 and 1936) required corroboration since they were so numerous and involved such a wide range of hosts. Through the kind co-operation of G. B. Thompson I have examined six specimens from the Zoological Museum, Helsingfors, all determined by Nordberg as *C. borealis*. Only one of these is in fact *C. borealis* (male) from the nest of the Fieldfare (*Turdus pilaris* L.) (Nystad). A male from the nest of the White Wagtail (*Motacilla alba* L.), a male and a female from the nest of the Fieldfare (*Turdus pilaris* L.) (Sakkola) and a male from the nest of the Meadow Pipit (*Anthus pratensis* (L.)) are all typical *C. garei*. In addition there is one female from the nest of the White Wagtail (*Motacilla d. alba* L.) which pertains to the *gallinae*-group, but is probably a hitherto undescribed species. F. G. A. M. Smit has kindly checked my determinations of these specimens.

[2] In 1908 James Waterston published a note in *Ann. Scot. nat. Hist.* **1908** : 257, which reads as follows : " *Ceratophyllus borealis* Rothsch., in Berwickshire.—From a single female taken in July 1906, by Mr. Joy in St. Kilda, Mr. Rothschild described the above species (*Ent. mon. Mag.*, Jan., 1907, p. 11). Since then no additional examples have occurred, but Mr. Rothschild refers to this name a male and two females of a *Ceratophyllus* taken on 28th May of this year, from a nest of *Cinclus aquaticus* on the Eye, near Granthouse. The male is now in Mr. Rothschild's collection and will be described shortly." However, only one atypical female specimen (see Rothschild, 1948) is in the C. Rothschild collection (B.M.) labelled from *Cinclus aquaticus* on the Eye, Granthouse, and when N. C. Rothschild described the male of this species (Rothschild, 1913) he selected a specimen from *Anthus obscurus* (= *spinoletta*), Haylor, Shetland. What became of the supposed male from *Cinclus aquaticus* (= *cinclus*) is not known. If it was indeed a typical *C. borealis* it seems unlikely that Charles Rothschild would have delayed his description of it until 1913.

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[3] This may have been a misleading caption (but see Appendix, p. 317) ; the text refers to the species as European.

[4] At the same time Allan examined six nests of the Fulmar (*Fulmarus glacialis* (L.)), three of the Eider Duck (*Somateria mollissima* (L.)), one of the Greater Black-backed Gull (*Larus marinus* L.), four of the Black-headed Gull (*Larus ridibundus* L.) and eight of the Herring Gull (*Larus argentatus* Pontop.), all of which were negative for fleas.

C. garei from Kugssuk, Godthaab Fjord, W. Greenland, from the nest of the Arctic Ptarmigan (*Lagopus rupestris* Gm.) collected by Major Kingston. These are the specimens referred to on p. 87 of my previous paper (Rothschild, 1948). Dr. K. Jordan re-examined these specimens for me at that time (letter dated 22nd September, 1947) and then considered them to be *C. garei.* ("I do not see any difference from European *C. garei,* which varies individually much more than some authors, e.g. Wagner, assumed.") Five additional specimens of this series are in the possession of the University Museum, Oxford. After re-examining the whole series together I have come to the conclusion that six of these specimens (four males and two females) are typical *C. garei*, but the remaining three females are intermediates showing degrees of variation in the direction of *C. borealis* (*see below*, p. 307). Finally Peus (1954) has published an extremely interesting record of a single typical *C. borealis* female from the nest of the Wheatear (*Oenanthe oenanthe* (L.)) from the mountains of Greece (Ossa, Kissawos, Thessaly—about 1000 metres).

ACKNOWLEDGMENTS

First and foremost I should like to thank the collectors who sent both specimens and birds' nests. It is perhaps not sufficiently appreciated that collecting is by far the most difficult and arduous part of parasitology. Kenneth Williamson's results in Fair Isle are quite outstanding, and the material sent by both J. F. Thomas and Lewis Davies has proved exceedingly interesting. I should also like to thank Ernest Goetz for some hazardous climbs on the railway buildings at Eigergletscher. I have received most valuable assistance from F. G. A. M. Smit, both with the determination of numerous specimens and the tracing of records. I am also grateful to S. M. D. Alexander, Ronald M. Allan, Theresa Clay, P. J. Condor, Lewis Davies, Richard Freeman, G. P. Holland, Ian Linn, David Stephen, G. B. Thompson and G. C. Varley for various records, the loan of specimens and information, and G. H. E. Hopkins, F. G. A. M. Smit and Kenneth Williamson for kindly reading and criticising the manuscript. I should also like to thank Arthur Smith for the excellent text figures. Rough sketches were made by the author, and a camera lucida used for the final drawings. Fig. 11 was executed by Enid M. Hayes from a list of localities obtained from specimens in the British Museum collection and the literature, and I should like to record my appreciation of the manner in which she has checked various obscure localities.

THE RECORDS FROM FAIR ISLE.[5]

Due to the highly successful collecting technique invented by Kenneth Williamson very numerous fleas were obtained from the bodies of birds trapped and subsequently examined in the laboratory on Fair Isle (details will be published elsewhere).

Fair Isle is situated twenty-four miles south-south-west from the southernmost point in the Shetlands, and twenty-six miles east-north-east of the most northerly point of the Orkneys. It is oblong in form, having an extreme length of about two-and-three-quarter miles from north to south and averaging about one mile in breadth. There are no trees or shrubs on the island, which is surrounded by precipitous cliffs 100 to 600 ft. high except in the extreme south-west. The northern two-thirds are mostly heathland. Fair Isle, as is well known, lies in the path of much European drift migration (Williamson, 1952 and 1953), and its isolated position turns it into a veritable bottleneck on autumn and spring passages for both continental and Greenland–Iceland birds.

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[5] Several of these records have already appeared in the *Fair Isle Bird Observatory Bulletin*, 1951–52.

Ceratophyllus borealis was obtained from the following species:

(A) *Migrants.*

Autumn passage:

Great Grey Shrike (*Lanius excubitor* L.) (1) (O'Mahony, 1949; specimen seen by the author).

Spring passage:

Willow Warbler (*Phylloscopus trochilus* (L.)) (1).
Whitethroat (*Sylvia communis* (Latham)) (2).
Greenland Wheatear (*Oenanthe oenanthe leucorrhoa* (Gm.)) (4).
Faeroe Wheatear (*Oenanthe oenanthe schioleri* Salomonsen) (2).
Sedge Warbler (*Acrocephalus schoenobaenus* (L.)) (1).
Whinchat (*Saxicola rubetra* (L.)) (1).
Redstart (*Phoenicurus phoenicurus* (L.)) (5).
Cuckoo (*Cuculus canorus* L.) (1).
Common Sandpiper (*Actitis hypoleucos* (L.)) (1).
Red-spotted Bluethroat (*Luscinia s. svecica* (L.)) (1).
White Wagtail (*Motacilla alba* L.) (1).
Grey Wagtail (*Motacilla cinerea* Tunst.) (1).
Pied Flycatcher (*Muscicapa hypoleuca* (Pall.)) (1).

This made a total of twenty-three records (32 specimens, of which 16 were males and 16 females).

(B) *Summer residents.*

Wheatear (*Oenanthe oenanthe* (L.)) (40).
Meadow Pipit (*Anthus pratensis* (L.)) (1).

This made a total of forty-one records (57 specimens, of which 29 were males and 28 females).

(C) *Residents.*

Blackbird (*Turdus merula* L.) (3).
Rock Pipit (*Anthus spinoletta* (L.)) (14).
Starling (*Sturnus vulgaris* L.) (1).
Eider Duck (*Somateria mollissima* (L.)) (from nest) (2).

This made a total of twenty records (21 specimens, of which 9 were males and 12 females).

Altogether *C. borealis* was obtained from the bodies of nineteen different species of hosts on Fair Isle. The number of spring migrants infested with this species is surprising, and it seems highly probable that all these birds, with the exception of the Greenland Wheatears and Wagtails, acquired these fleas after arrival on the island.

Kenneth Williamson also obtained on Fair Isle fourteen nests of the Wheatear, collected shortly after the young had flown, and which he sent to A. R.

Edwards or myself. Fleas were collected from them for the next four to six months as they hatched out, but it was not possible to collect all the fleas from the nests sent to me ; merely a representative sample was obtained. A total of 1331 specimens of *C. borealis*, 550 males and 781 females was collected (see footnote 10), or a mean of 95 fleas per nest. The estimated number of breeding pairs of Wheatears on Fair Isle is 800 (Alec Butterfield, 1953, *Fair Isle Bird Obs. Bull* **8** : 9–10), and therefore it seems permissible to assume that a *C. borealis* population of at least 75,000 must be present in the nests of this species during and after the breeding season. There can be little doubt that this is an under-estimate ; Thompson (1954) found that 352 was the average number of fleas per nest (eight examined) of the Wheatear on Skokholm Isle. It will be recalled that both in Iceland (Lindroth, 1931) and Greenland (present paper) *C. borealis* was found free on the ground. It is not difficult to imagine that new bird-arrivals on the island, walking about and feeding on the ground, would pick up stragglers of this species. Ioff (1941) recorded large numbers of *Ceratophyllus* migrating out of burrows at night ; this habit may well be characteristic of other species, such as *C. borealis*, and would naturally aid in their dispersal about the island. Condor (*in* Thompson, 1954) notes that the Wheatear does not occupy the same nesting burrow for two consecutive years. Migrations from the burrows and scattering of the adult fleas would therefore constitute an adaptation to the life of this particular host.

It should be emphasised that among approximately 1400 specimens of *C. borealis* no intermediates between this species and *C. garei* were found. All may be described as typical *C. borealis*. We also examined seven nests of the Eider Duck. Only two of these contained fleas—a single typical *C. borealis* female in each case. These are the first records of *borealis* from any of the ducks.

The comparative scarcity of *C. garei* on Fair Isle.

It will be recalled that *C. garei* is a Holarctic species with a marked northerly distribution, widespread across the northern part of North America from Hudson Bay to Alaska (Holland, 1949) and from north central Europe northwards (K. Jordan, 1932 ; M. Rothschild, 1948, 1952). It is very common on the mainland of Britain (Rothschild, 1952), and its range overlaps with that of *C. borealis* in Finland, Iceland, Greenland and in the Shetland Isles. It is quite common in the Orkney Islands, from which hitherto there have been no records of *C. borealis*. It is also apparently absent from Ushant, the Alps and the Scilly Isles and other small islands round the west coast of Britain. On Fair Isle *Dasypsyllus g. gallinulae* Dale (1878) and *Ceratophyllus gallinae* Schrank (1803) were found on resident, summer resident and migrant birds, but until August, 1953, there had been no trace of *C. garei*. On 7th August, 1953, one male specimen of this flea was taken from a Meadow Pipit.[6] Kenneth Williamson informs me that at this time there was undoubtedly a migratory movement in progress, and eleven Meadow Pipits were taken in the traps on the 6th August, all weighing around 17 to 19 grams. This could have been a purely local movement, or an influx from Shetland. It was interesting, however, that the bird which harboured *C. garei* weighed only 15 grams—considerably lighter than any bird ringed during early and mid July, from which it would appear probable that this juvenile was not a local bird, though there can of course be no certainty. In the spring of 1954 two further specimens of *C. garei*, both females, were recorded from the bodies of migrants, one from the White Wagtail (*Motacilla alba* L.) and the other from the Woodcock (*Scolopax rusticola* (L.).

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[6] In 1906 and 1912 Eagle Clarke did not record the Meadow Pipit as a species breeding on Fair Isle. If this is correct and it has only begun to nest on the Island since that date, it would be the most likely bird to introduce *C. garei* as a resident species of flea on to Fair Isle.

During the summer Kenneth Williamson kindly sent me several nests of the Meadow Pipit, which is a host for *C. garei* in the Shetland Isles, the Isle of Wight and Foulness Isle. But these nests from Fair Isle were completely negative. The most significant fact was the absence of *C. garei* and the presence of *C. borealis* in the nests of the Eider Duck, since this bird is one of the favoured hosts of *C. garei* in Iceland, and this flea is also recorded from it from the Orkney Isles, the Bass Rock and the Farne Islands (Bagnall, 1919) (specimens in the N. C. Rothschild collection). Further collecting is required, but nevertheless it seems probable that *C. garei* is absent from resident birds on Fair Isle, not only apparently so. The absence of any trace of intermediates in the *borealis* populations of Fair Isle suggests that if it has become established on the island its introduction must have occurred very recently.

NEW RECORDS OF *C. BOREALIS* ON THE MAINLAND OF BRITAIN

The most interesting aspect of the records from the mainland is the fact that in four out of the nine nests in which this species was found *C. garei* was also present. The relative numbers were as follows :

	C. borealis.		*C. garei.*		*Intermediates.*	
	♂	♀	♂	♀	♂	♀
Moorhouse Nature Reserve, Alston, Cumberland :						
(1) Grey Wagtail's nest (1670 ft. altitude)	2	1	5	10	—	1
(2) Ring Ousel's nest (1520 ft. altitude)	1	—	4	2	—	2
(3) Wheatear's nest . . .	15	23	—	—	—	—
(4) Meadow Pipit's nest* . . .	2	—	—	—	—	—
Laugharne Burrows, Carmarthenshire :						
(1) Whinchat's nest (approx. 20 ft. altitude)	—	1	48	44	1	1
(2) Wheatear's nest 1 (approx. 20 ft. altitude)	10	7	—	—	—	—
(3) Wheatear's nest 2 (approx. 20 ft. altitude)	5	15	—	—	—	—
(4) Wheatear's nest 3 (approx. 20 ft. altitude)	17	13	1	1	—	—
(5) Wheatear's nest	7	12	—	—	—	—

* A Meadow Pipit's nest from Laugharne Burrows, Carmarthenshire, contained only *C. garei.*

Two Skylark's nests and two Curlew's nests were negative for fleas. It will be recalled that in the nest of the Herring Gull in which Waterston collected one intermediate female (Rothschild, 1948) a typical male specimen of *C.*

garei was also found. Likewise in the same nest of the Wheatear from Derbyshire in which Thompson discovered his single specimen of a male *C. borealis*, *C. garei* was also present.[7] The same applies to the single female from the nest of the Grey Wagtail (*see above*, p. 296) from Loganlea Waterfall. There seems to be every reason to believe that the two species can interbreed and, if the opportunity presents itself, actually do so and produce hybrids.

It should also be noted that all the mainland records come from moorland districts or coastal areas, rather similar to the country encountered on such islands as Fair Isle and Ushant. Since spring migrants passing through Fair Isle have a good chance of acquiring new infestations of *C. borealis* they probably also from time to time carry them on to their breeding haunts. This would apply especially to such birds as the Greenland Wheatear.

In a personal communication Mr. Condor has informed me that at least one Wheatear colour-ringed on Skokholm has been known to nest on the mainland of Pembrokeshire. In this manner *C. borealis* may not infrequently be reintroduced into " Wheatear " country on the mainland of Britain.

The Intermediates.

In the case of the intermediates it is not possible to say to which of the two species the specimens in question pertain. Some specimens veer towards one species more than the other. In the male of *C. borealis* the roughened spiculose area on the inside of tergum VIII (fig. 6) is more extensive than in *C. garei*, a few spicules reaching well beyond the last strong marginal bristle. In *C. garei* this area is narrower (confined to the margin in most specimens), and the individual spicules are much smaller, and rarely extend beyond the third marginal bristle (fig. 6, *d*). In the *Synopsis of the British Siphonaptera* (1915) Rothschild (p. 68) states that in *C. garei* the eighth tergite " is *without* an internal area of sharp points, only a few such raised points being present at or close to the margin ", but I have found that there is some slight variation in this character (fig. 6, *d*), and a few specimens can be said to have a spiculose area, though very greatly reduced (neither of K. Jordan's drawings in Rothschild 1906 and 1915 illustrates this particular feature.)[8] In intermediate specimens the spiculose area falls midway between the two in character (fig. 6, *a*), both with regard to the extent of the area itself and the development of the individual spicules. Another character by which males of the two species can usually be separated is the apical membranous appendage (" flap " of Rothschild, 1915) of st. VIII. In *C. borealis* the apical or distal edge (which is finely serrated) is strongly excised (concave), and where the appendage joins the terminal portion of st. VIII[9] it is set with small points or spicules (fig. 2, *a*, *c*). In *C. garei* this apical or distal edge (which is also serrated, but very finely and only at the extreme border) is expanded into a full convex curve, so that the whole appendage is roughly circular in outline instead of triangular (figs. 2, *b*; 3). The basal or proximal edge of the membraneous appendage bears a thumb-like outgrowth in

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[7] Through the kindness of G. B. Thompson I have seen these specimens.

[8] Since the completion of this paper a good drawing has appeared in Smit's Lopper (Siphonaptera), *Danmarks Fauna* **60**, figures 177–182.

[9] In Rothschild's description of the male of *C. borealis* (*Ent. mon. Mag.*, 1913, 2nd series, Vol. XXIV, p. 182) st. VIII is accidentally referred to as st. IX in the text, though correctly labelled in the figure.

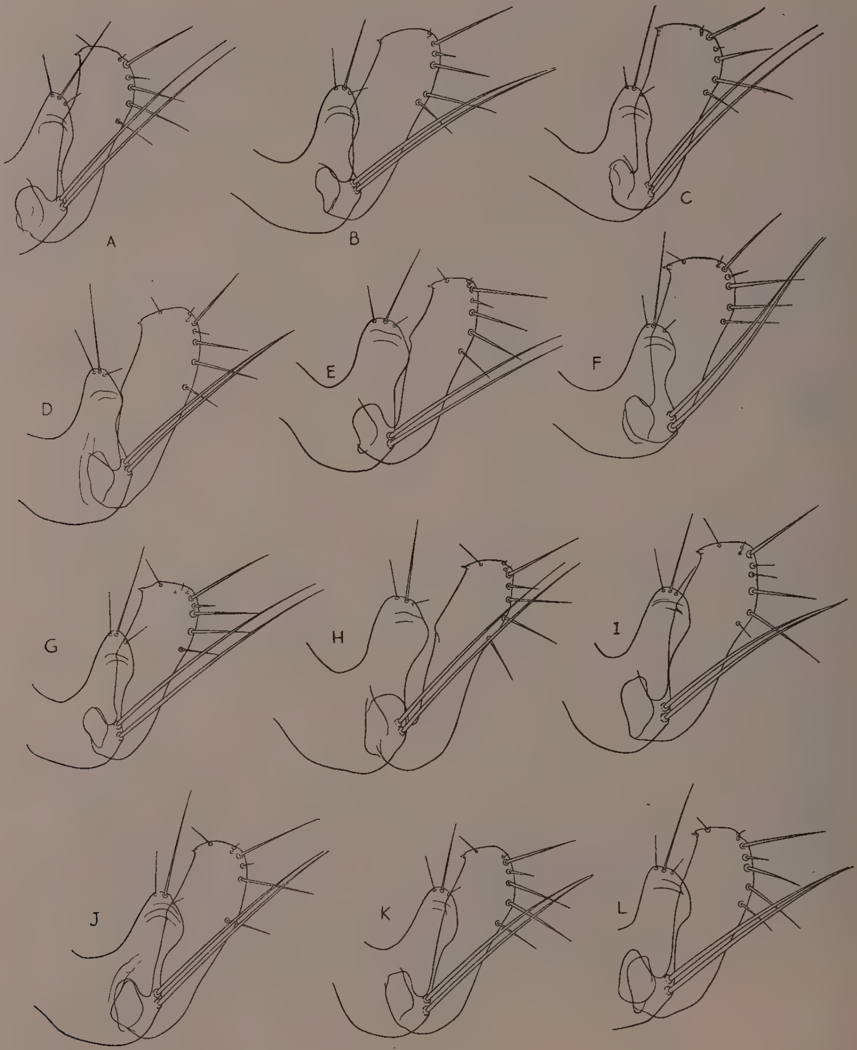

FIG. 1.—Movable process (P^3) and fixed process (P^1) of claspers (only the principal bristles have been drawn in). (*a*) Intermediate between *C. garei* and *C. borealis* from nest of *Saxicola rubetra*, Laugharne Burrows, Carmarthenshire, Wales. (*b*) *C. garei* from nest of *Fringilla** (= *Carduelis*) *cannabina* and *Parus major*, Wulfsdorf, Lubeck, Germany. (*c*) *C. garei* from nest of *Motacilla alba*, Nystad, Finland. (*d*) *C. garei* from nest of *Lagopus rupestris*, Kugssuk, Godthaab Fjord, West Greenland. (*e*) *C. borealis* from nest of *Oenanthe oenanthe*, Inishtrahull, Co. Donegal, Ireland. (*f*) *C. garei* from nest of *Anthus pratensis*, Muonio, Finland. (*g*) *C. garei* from nest of *Linota* (= *Carduelis*) *cannabina*, Newport, Isle of Wight. (*h*) *C. borealis* from nest of *Anthus obscurus*, Haylor, Shetland. This illustrates the extreme "*borealis*" type.

C. garei (fig. 2, *b*; 3), but in most specimens of *C. borealis* this is lacking, although it is very occasionally present in a stunted form (fig. 2, *c*). In the intermediate specimens the terminal portion of st. VIII combines the characters of both species (fig. 2, *d*). In *C. borealis* the curved portion of the crochet (of the phallosome) is more evenly attenuated and more sickle-shaped than in *C. garei*, but ending in a rounded tip (fig. 4, *e*, *h*, *i*, *k*, *l*). In *C. garei* it is broader at the base, not so evenly sickle-shaped, and with a sharply pointed tip (fig. 4, *b*, *c*, *d*, *f*, *g*, *j*). In intermediate specimens these two shapes merge and cannot be separated (fig. 4, *a*).

These characters are not, of course, a complete list of the morphological distinctions between the males of these two species; they have been selected chiefly because they can be seen in unmounted material. A comparison of fig. 1, *a* to *l* will demonstrate, for instance, that the claspers also show considerable differences. Thus in *C. garei* the fixed process is shorter and has a narrower and more conical apex. The movable process of the clasper has a small notch or bulge (an incipient "locking" device) on the anterior margin. In *C. borealis* (fig. 1, *e*, *h*, *i*, *k*, *l*) the part of the process below this notch is much longer in proportion than in *C. garei* (fig. 1, *b*, *c*, *d*, *f*, *g*, *j*). The distal portion of the apical arm of st. IX is more curved in *C. borealis* (fig. 5, *e*, *h*, *i*, *k*, *l*), and the angle of the dorsal margin (fig. 6, *b*) of t. VIII is more distinct. There are various other distinctions which separate the two species, but none of these will serve to enable the intermediate specimens to be referred with confidence to either species.

In the case of the female intermediates the projection or lobe (fig. 8, *k*–*n*) present on the margin of the seventh sternite in typical *C. borealis* (fig. 8, *o*–*v*) and lacking in *C. garei* (fig. 8, *a*–*j*) is greatly reduced, and the outline is in fact precisely intermediate between the two. Sometimes on one side of a specimen it veers towards the condition typical of *borealis*, and on the other side of the same specimen towards *garei*. The spermatheca in typical *C. borealis* has a terminal papilla situated at the end of the tail (figured in Rothschild, 1915, but not mentioned in the text). It is lacking in *C. garei*, but intermediate specimens (fig. 7, *f*–*h*, *n*) generally bear a suggestion of this papilla in varying degrees.

The shape and proportions of the normal spermatheca are shown in fig. 7, *a*–*e*, *i*–*m*, *o*. It is rather difficult to convey these differences in a written description. The spermatheca of *C. garei* is generally larger, although the ratio of tail : head is less than in *C. borealis* (fig. 7, *i*–*m*, *o*). The tail is more sausage-shaped or teat-like in *C. garei*, whereas in *C. borealis* it is widest near the middle and then narrows again, thus appearing distinctly tapered. Generally the upper

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(*i*) *C. borealis* from nest of *Saxicola* (= *Oenanthe*) *oenanthe*, St. Mary's, Scilly Isles. (*j*) *C. garei* from nest of *Fuligula* (= *Aythya*) *marila*, Myvatn, N. Iceland. In this specimen the shape of P^1 veers towards that found in *C. borealis*. (*k*) *C. borealis* from nest of *Turdus pilaris*, Nystad, Finland. This illustrates a somewhat conical P^1 veering towards the *garei* type. (*l*) *C. borealis* from body of *Anthus pratensis*, Ushant, France.

The following points should be noted: the conical shape of P^1 and the relatively broader, shorter movable process in *C. garei*. The most extreme type of *C. borealis* is shown in the specimen from Haylor, Shetland, in which the movable process (P^3) is four times as long as broad. In *C. garei* it is approximately three times as long as broad.

* Host names as shown on the slide of the specimen concerned.

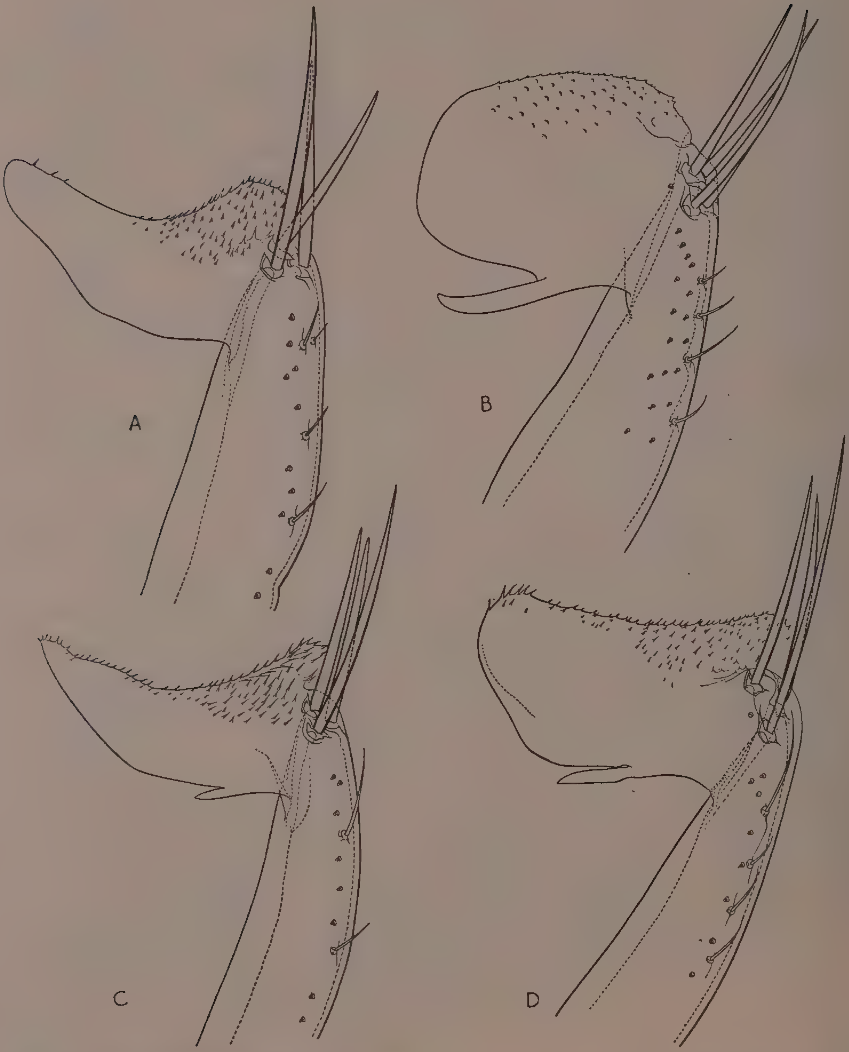

Fig. 2.—Terminal portion of st. VIII with apical appendage. (Note the variation of the terminal bristles.) (*a*) *C. borealis* from *Oenanthe oenanthe*, Fair Isle. (*b*) *C. garei* from nest of *Fuligula* (= *Aythya*) *marila*, Myvatn, N. Iceland. (*c*) *C. borealis*† from body of *Oenanthe oenanthe*, Ushant, France. Note the incipient "thumb" on the ventral margin of the apical appendage. (*d*) Intermediate between *C. garei* and *C. borealis* from nest of *Saxicola rubetra*, Laugharne Burrows, Carmarthenshire, Wales.

† A series of *borealis* showing this character was obtained by G. B. Thompson from the nest of the Wheatear on Skokholm Isle. It has never been noted on specimens from Fair Isle.

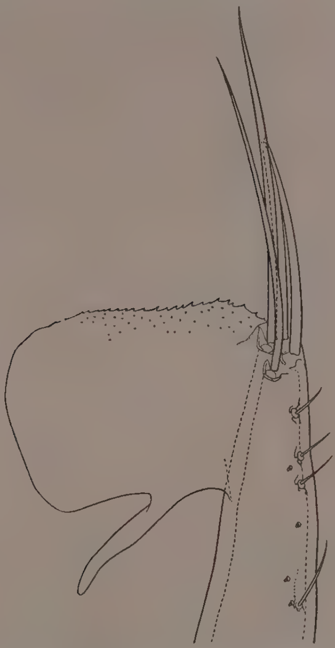

FIG. 3.—Terminal portion of st. VIII with apical appendage of *C. garei* from nest of *Fringilla* (= *Carduelis*) *cannabina* and *Parus major*, Wulfsdorf, Lubeck, Germany.

side of the head of the spermatheca in *C. garei* is distinctly concave and the underside strongly convex—somewhat the shape of an old-fashioned baby's feeding bottle. In the case of *C. borealis* the upper margin is barely (if at all) concave, and the head as a whole is roughly barrel-shaped. The sclerotisation of the wall of the head is certainly more pronounced in *C. garei*, but, since the apparent degree of sclerotisation varies according to the method used in mounting, this character is difficult to assess. In the intermediate females (fig. 7, *f–h*, *n*) the shape and proportions of the spermatheca fall midway between these types.

The males in the series from the nest of *Lagopus rupestris* from West Greenland are *C. garei*—at least I personally would have little hesitation in determining them as such (figures 1, *d*; 4, *d*; 5, *d*; 6, *c*), and as I have stated on page 297 this was also Dr. Jordan's view in 1947 when I drew his attention to these specimens, which were at that time labelled "*borealis*". The spiculose area of t. VIII in particular is very much reduced; in fact it can be said to be far less conspicuous than in many specimens from the mainland of Europe.[10] The

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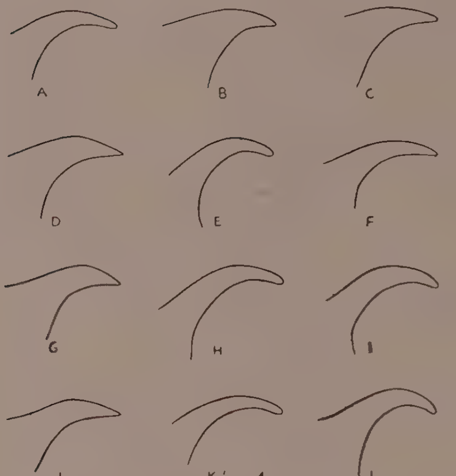
[10] Dr. E. B. Ford has drawn my attention to the fact that throughout the area where the ranges of the two subspecies overlap and interbreeding occurs one can expect to find not only intermediates, but also specimens in which the typical specific distinctions are exaggerated, for example *garei* with a smaller spiculose area than is usual and *borealis* with a larger spiculose area than is usual. He has also pointed out that an abnormal excess of females in the intermediates is to be expected in crosses between subspecies if the male is the heterogamic sex. However, the figures obtained give a significant excess of females



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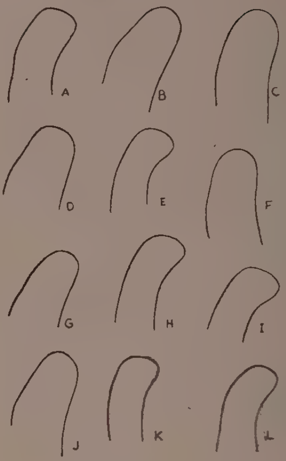

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Figs. 4–5.—(4) Terminal portion of crochet of phallosome in: (*a*) Intermediate between *C. garei* and *C. borealis* from nest of *Saxicola rubetra*, Laugharne Burrows, Carmarthenshire, Wales. (*b*) *C. garei* from nest of *Fringilla* (= *Carduelis*) *cannabina* and *Parus major*, Wulfsdorf, Lubeck, Germany. (*c*) *C. garei* from nest of *Motacilla alba*, Nystad, Finland. (*d*) *C. garei* from nest of *Lagopus rupestris*, Kugssuk, Godthaab Fjord, West Greenland. (*e*) *C. borealis* from nest of *Oenanthe oenanthe*, Inishtrahull, Co. Donegal, Ireland. (*f*) *C. garei* from nest of *Anthus pratensis*, Muonio, Finland. (*g*) *C. garei* from nest of *Linota* (= *Carduelis*) *cannabina*, Newport, Isle of Wight. (*h*) *C. borealis* from nest of *Anthus obscurus*, Haylor, Shetland. (*i*) *C. borealis* from nest of *Saxicola* (= *Oenanthe*) *oenanthe*, St. Mary's, Scilly Isles. (*j*) *C. garei* from nest of *Fuligula* (= *Aythya*) *marila*, Myvatn, N. Iceland. (*k*) *C. borealis* from nest of *Turdus pilaris*, Nystad, Finland. (*l*) *C. borealis* from body of *Anthus pratensis*, Ushant, France.

Note the wider base and pointed apex in *C. garei*, and the more pronounced sickle-shaped curve and rounded tip in *C. borealis*. In (*f*) the shape veers towards that of the intermediate (*a*).

(5) Terminal portion of st. IX in: (*a*) Intermediate between *C. garei* and *C. borealis* from nest of *Saxicola rubetra*, Laugharne Burrows, Carmarthenshire, Wales. (*b*) *C. garei* from nest of *Fringilla* (= *Carduelis*) *cannabina* and *Parus major*, Wulfsdorf, Lubeck, Germany. (*c*) *C. garei* from nest of *Motacilla alba*, Nystad, Finland. (*d*) *C. garei* from nest of *Lagopus rupestris*, Kugssuk, Godthaab Fjord, West Greenland. (*e*) *C. borealis* from nest of *Oenanthe oenanthe*, Inishtrahull, Co. Donegal, Ireland. (*f*) *C. garei* from nest of *Anthus pratensis*, Muonio, Finland. (*g*) *C. garei* from nest of *Linota* (= *Carduelis*) *cannabina*, Newport, Isle of Wight. (*h*) *C. borealis* from nest of *Anthus obscurus*, Haylor, Shetland. (*i*) *C. borealis* from nest of *Saxicola* (= *Oenanthe*) *oenanthe*, St. Mary's, Scilly Isles. (*j*) *C. garei* from nest of *Fuligula* (= *Aythya*) *marila*, Myvatn, N. Iceland. (*k*) *C. borealis* from nest of *Turdus pilaris*, Nystad, Finland. (*l*) *C. borealis* from body of *Anthus pratensis*, Ushant, France.

Note the lack of incurving below the tip in *C. garei*, thus giving st. IX a wider appearance.

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not only in the intermediates but also in the pure *C. borealis* populations from nests on Fair Isle (see page 299). It is therefore not clear that the real departure from equality in the relative numbers of the sexes of the intermediates reflects a subspecific or specific difference between *C. borealis* and *C. garei* since there could well be a constant preponderance of females in the sex-ratio of this species.

apical membraneous appendage of st. VIII is also typical of *C. garei*, with a thumb-like outgrowth on the ventral margin and an almost entire dorsal margin. The crochet of the phallosome is not sickle-shaped and has a pointed apex. The apex of the fixed process is narrow (fig. 1, *d*). The female specimens from this series, however, present a different picture. Although two may be regarded as fairly typical *C. garei*, one should be described as *C. garei* showing certain characters veering towards *borealis*, and two others are almost perfect intermediates (fig. 7, *n*) between the two species. It would therefore appear that also on the mainland of Greenland these two species interbreed and further collecting will almost certainly demonstrate that hybrids occur wherever the range of the two species overlaps, in Holland, Britain, Finland, Iceland, Greenland, and also the mainland of Canada, although up to the present *C. borealis* has not been recorded west of Greenland. In fact specimens of either species found in the nest with intermediates must always be regarded with suspicion, and it seems likely that the males of *C. garei* from the above-mentioned nest of *Lagopus rupestris* are not pure *garei* although they appear to be so. It is worth noting that among the 13 obvious intermediates mentioned in this paper, from Greenland as well as the British Isles, only one specimen is a male (see footnote 10).

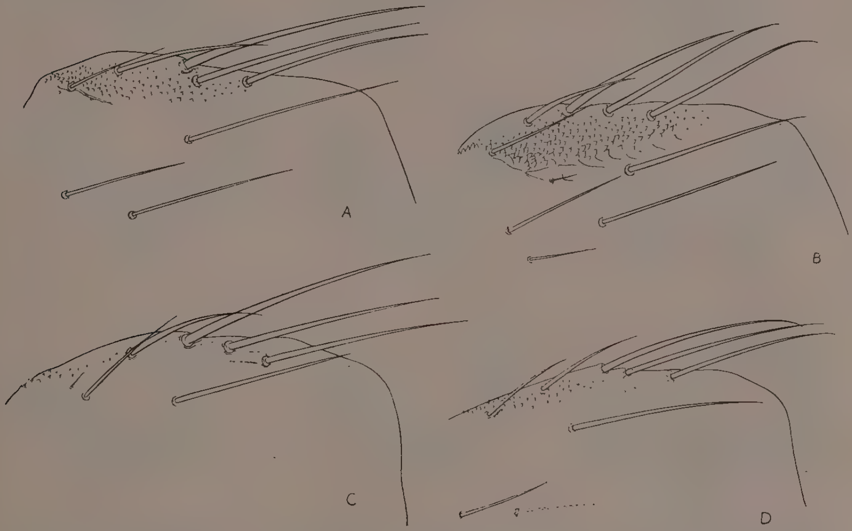

Fig. 6.—Dorsal margin of t. VIII showing spiculose area. (Note the variation in the arrangement of the marginal bristles.) (*a*) Intermediate between *C. garei* and *C. borealis* from nest of *Saxicola rubetra*, Laugharne Burrows, Carmarthenshire, Wales. (*b*) *C. borealis* from body of *Oenanthe oenanthe*, Ushant, France. (*c*) *C. garei* from nest of *Lagopus rupestris*, Kugssuk, Godthaab Fjord, West Greenland. (*d*) *C. garei* from *Panurus biarmicus*, Hickling Broad, Norfolk.

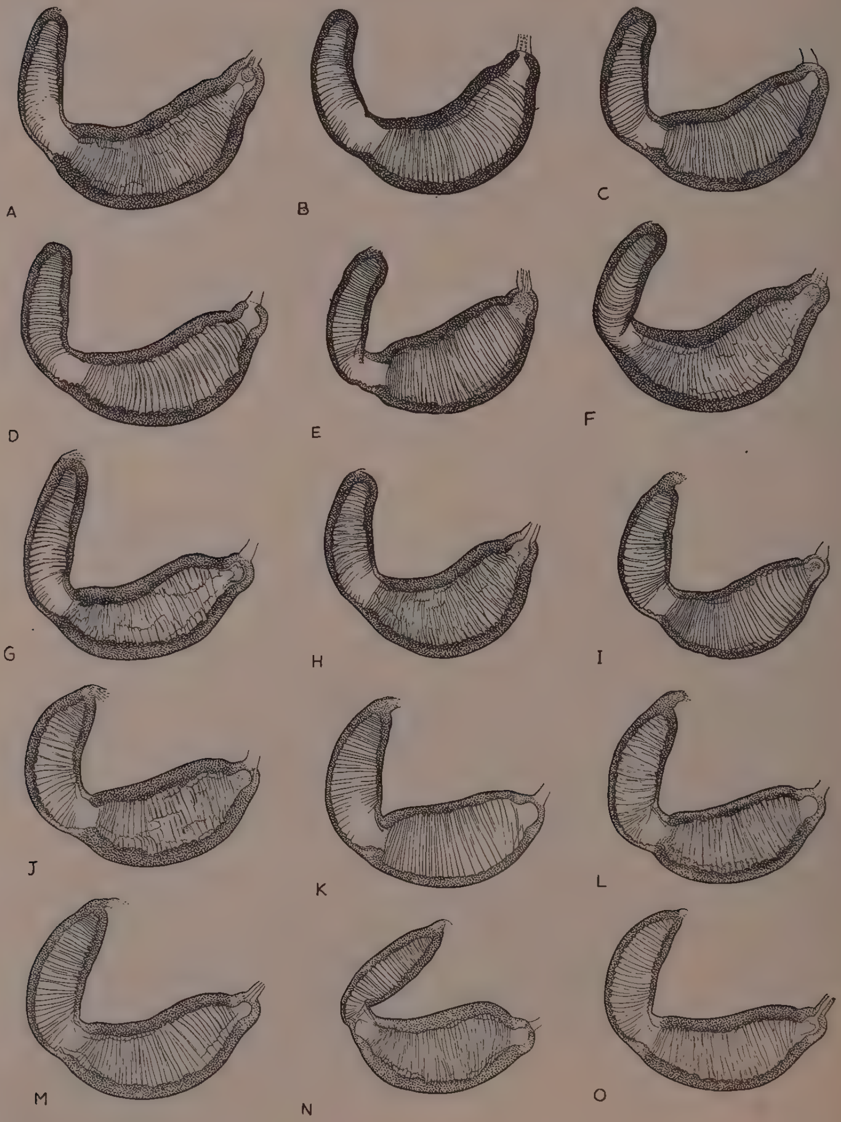

FIG. 7.—Spermatheca of *C. garei*, intermediates, and *C. borealis*. *C. garei* (*a*) from *Larus fuscus*, Walls, Shetland; (*b*) from nest of *Motacilla cinerea*, Alston, Cumberland; (*c*) from nest of *Gallinula chloropus*, Ashton, Peterborough; (*d*) from nest of *Motacilla cinerea*, Alston, Cumberland; (*e*) from nest of *Gallinula chloropus*, Tring, Herts.

Intermediates from nest of (*f*) *Turdus torquatus*, Alston, Cumberland; (*g*) *Motacilla cinerea*, Alston, Cumberland; (*h*) *Motacilla cinerea*, Alston, Cumberland; (*n*) *Lagopus rupestris*, Kugssuk, Godthaab Fjord, West Greenland.

C. borealis from (*i*) *Oenanthe oenanthe*, Fair Isle, Scotland; (*j*) nest of *Anthus obscurus*, Shetland Isle; (*k*) *Phoenicurus phoenicurus*, Fair Isle, Scotland; (*l*) *Oenanthe oenanthe*, Fair Isle, Scotland; (*m*) *Anthus obscurus*, Haylor, Shetland Isle; (*o*) *Motacilla cinerea*, Alston, Cumberland.

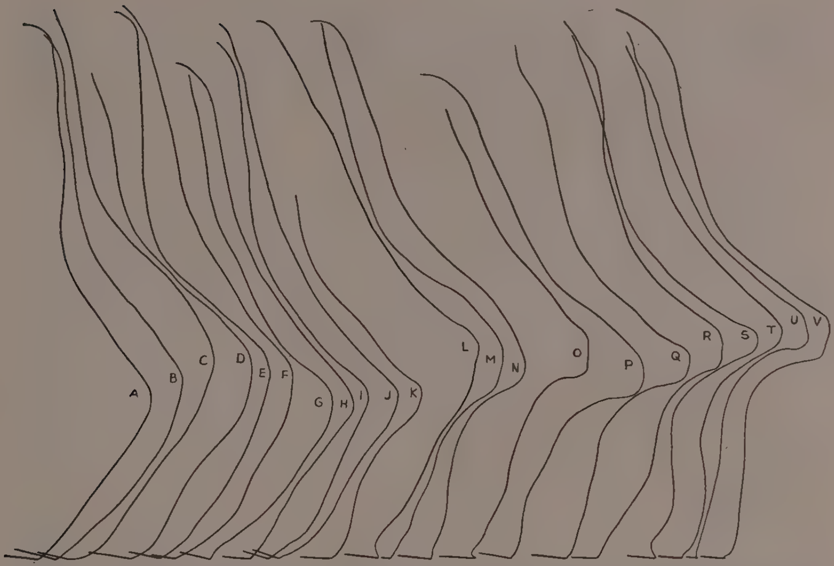

FIG. 8.—Outlines of st. VII in *C. garei* (*a*–*j*), in specimens showing characters intermediate between *C. garei* and *C. borealis* (*k*–*n*) and in *C. borealis* (*o*–*v*). (*a*) From *Panurus biarmicus*, Hickling Broad, Norfolk. (*b*)* From *Corvus corone*, Ashton, Peterborough, Northants. (*c*) From *Larus fuscus*, Walls, Shetland. (*d*) From *Motacilla cinerea*, Alston, Cumberland. (*e*) From *Gallinula chloropus*, Ashton, Peterborough. (*f*) From *Motacilla cinerea*, Alston, Cumberland. (*g*) From *Motacilla cinerea*, Alston, Cumberland. (*h*) From *Gallinula chloropus*, Tring, Hertfordshire. (*i*) From *Motacilla cinerea*, Alston, Cumberland. (*j*) From *Motacilla cinerea*, Alston, Cumberland. (*k*) From *Turdus torquatus*, Alston, Cumberland. (*l*) From *Turdus torquatus* Alston, Cumberland. (*m*) From *Turdus torquatus*, Alston, Cumberland. (*n*) From *Motacilla cinerea*, Alston, Cumberland. (*o*) From *Oenanthe oenanthe*, Fair Isle, Scotland. (*p*) From *Oenanthe oenanthe*, Fair Isle, Scotland. (*q*) From *Anthus obscurus*, Shetland. (*r*) From *Oenanthe oenanthe*, Fair Isle, Scotland. (*s*) From *Phoenicurus phoenicurus*, Fair Isle, Scotland. (*t*) From *Oenanthe oenanthe*, Fair Isle, Scotland. (*u*) From *Anthus obscurus*, near Haylor, Shetland. (*v*) From *Sylvia communis*, Fair Isle, Scotland.

* A photograph of the spermatheca of this specimen can be seen on plate XIIIa, *Fleas, Flukes & Cuckoos* (M. Rothschild & T. Clay, 1952).

THE DISTRIBUTION OF *C. BOREALIS*.

It may be recalled that in the previous paper the author suggested that *C. borealis* is a " fringing form " which has been displaced over the greater part of its range by the very closely-related *C. garei*. This term was coined by O. W. Richards (1935) to describe a type of distribution in which representatives of an older wave of colonisation have been displaced by related forms belonging to a more recent central European fauna and have only maintained themselves in isolated localities in marginal areas. Peus (1954) supports this suggestion. Discussing this type of distribution Zimmermann (1950) writes : " As the driving force of recent forms has in the main been directed from the east and south towards the west and north, the refuges of the older fauna are found at the north-west edge of Europe. . . . The fact that the refuges of fringing forms include such big climatic contrasts as . . . the central Alps and the Channel Isles, or the Channel Isles and the Orkney Isles, distinguishes fringing distribution from other types of distribution, such as the boreo-British of C. Lindroth or the well-known boreo-Alpine ; the causal explanation of these latter types is based on the climatic factors which the separated areas have in common."

Beirne (1952) suggests that the Bumble Bee, *B. smithianus* (with which the distribution of *C. borealis* was compared in my previous paper), is a " Celtic Land " population of *B. muscorum*. Discussing on p. 94 the survivors of the " Celtic Land " populations in Britain, he states : " . . . the British Isles were invaded from the continent by other populations of the same species. These spread northwards and westwards. Eventually the ranges of the two populations of each species met. Interbreeding or competition between them took place. As the more recent invaders were more abundant than the Celtic Land populations the latter were gradually absorbed or driven back. They now survive only in remote parts of the mainland into which the more recent invaders have not yet had time to spread or in islands that have become isolated from the mainland by the sea by the time the more recent invaders had reached their neighbourhood."

It seems not unlikely that *C. borealis* was originally also a " Celtic Land " survivor, but one which spread with its hosts into the British Isles via the loess steppe of north central Europe, and should be described as a glacial phase rather than a temperate phase invader (see Beirne, p. 81).

The fact that *C. borealis* is so abundant on Fair Isle, whereas *C. garei* is so rare, is particularly interesting. This latter species is common on the groups of larger islands, the Shetlands lying to the north and the Orkneys to the south, but appears to have failed hitherto to establish itself on the " isolated outpost " of Fair Isle which lies midway between the two. Another point worth noting is that on the islands off the east coast of Britain, such as Foulness Isle, the Bass Rock and the Farne Islands, *C. garei* is present and *borealis* has not yet been found. Even more interesting, perhaps, is the fact that in the moorland areas on the mainland and even in the nest of the preferred host of *C. borealis* (the Wheatear), *C. garei* is also present and crossing occurs between the two species. This certainly suggests that even in oecological conditions which are most favourable to *C. borealis* this species is gradually being eliminated by *C. garei*.

Beirne (p. 95) considers that in most animals interbreeding is a more important factor than competition in causing the extermination of " Celtic Land " subspecies.[11] In the case of *C. borealis* competition from species other than *C. garei* may also play a part. It is interesting to note, for instance, that *C. borealis* is the parasite of the House Sparrow (*Passer domesticus* L.) on Ushant, but not on Fair Isle, where *C. gallinae* is found on this host. At Eigergletscher (2320 metres) *C. borealis* was present in high aerial nests of the Snow Finch—i.e. nests placed under eaves and slates on the roofs and sides of tall buildings. Dr. Jordan collected it from the nests of the Black Redstart (*Phoenicurus ochrurus* (Gm.)) in the Haute Savoie (1400 metres)—a bird which also nests on or in buildings in the mountains, whereas at slightly lower altitudes at Wengen (1274 metres) the author found only *C. gallinae* in the nests of this bird. It therefore seems possible that *C. borealis* has been restricted to ground-nesting

[11] The term used by Beirne is " races ".

species of host by competition from fleas such as *C. gallinae*, which are better adapted to aerial nests, but in areas to which *C. gallinae* has not been able to penetrate it can still breed successfully on a wide range of hosts including those which build under roofs in dry situations. Interbreeding with *C. garei*, however, is probably the most important factor concerned in its extermination on the mainland.

In almost all cases it would appear that a " fringing distribution " when displayed by a flea must have an oecological rather than an historical explanation. One would expect the flea to be carried rapidly all over the area occupied by the host or hosts unless some factor, for instance the humidity or temperature requirements of the larval stages, restricts its distribution to certain areas of the host's range. In other instances one might also suppose that a " fringing form " of flea would reflect the past or present history of the host. This would apply particularly to species which are markedly host-specific. The circumstances, however, in the case of *C. borealis* and *C. garei* are rather unusual, and it seems quite possible that we have here a genuine example of replacement by an invading species or subspecies of flea.

Should one, however, consider *C. borealis* and *C. garei* as distinct species or as two subspecies of the same flea? The character of the eighth sternites in the males and the spermathecae in the females, and other less important characters, suggest that we are here concerned with two very closely related but different species. This was Dr. Jordan's view in 1947, when the question was put to him—a time at which we had far less material available for comparison. In a letter in which he expressed this opinion he opened with the following general remarks : " The basis of systematics is the knowledge of the latitude of the individual variability of subspecific and specific populations. This knowledge can only be acquired by the study of large series of specimens." Later (letter of 12th July, 1954) he added that if it was a fact that the two insects occupied different areas " a taxonomist would be justified in treating them as subspecies—a simplification of classification, nothing else. When the details of the life cycle become known *borealis* and *garei* may be proved to be independent species."[12] Peus (1954) considers that in all probability the two fleas are subspecies, and he does not think the morphological differences sufficiently pronounced to prove a serious stumbling-block to the acceptance of this theory. The free interbreeding which occurs where the ranges of the two fleas overlap seems to favour this view. The morphological differences are, however, more marked than those which generally distinguish subspecies in this genus. Peus, furthermore, points out that the classical concept of a fringing distribution is one in which one *subspecies* displaces another. Although this is absolutely correct, it is also quite possible to conceive of two such subspecies diverging and differentiating sufficiently to attain—through isolation or some similar factor—the rank of species before the displacement of the one by the other occurs. However, if we examine the few figures on p. 302 it must be agreed that both *C. borealis* and *C. garei* show very considerable variation ; more collecting and a more critical examination of large series of specimens, together with breeding experiments, will be necessary before we can satisfy Dr. Jordan's criteria for deciding the status of these two fleas.

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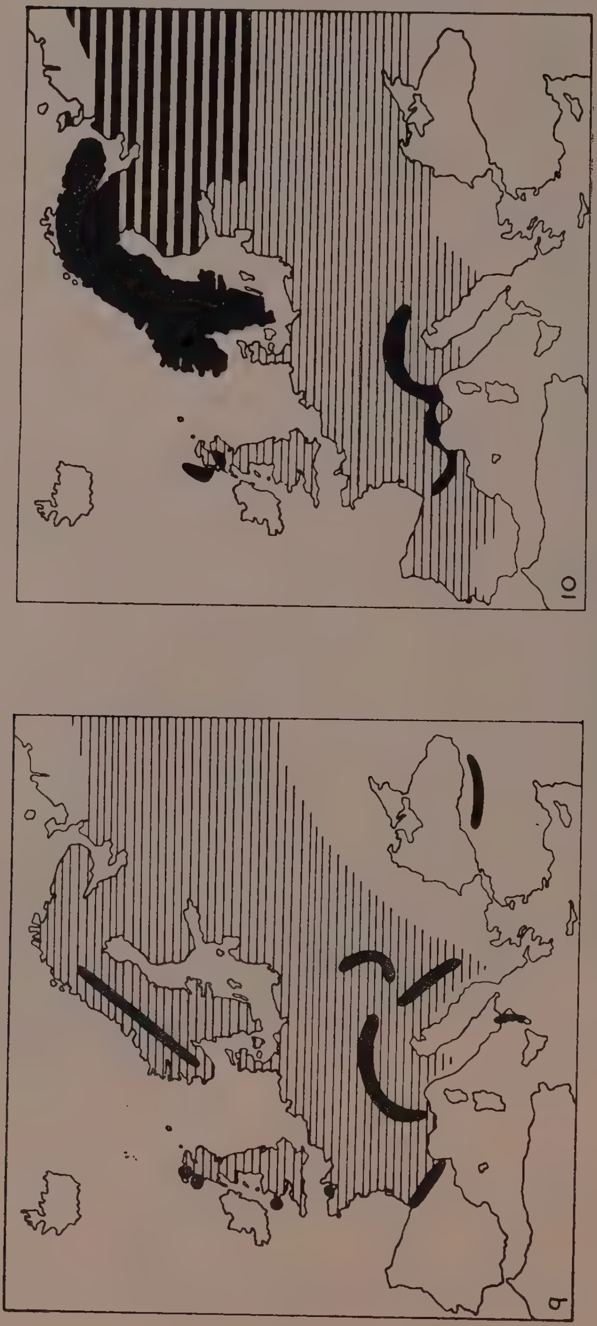
[12] Dr. Jordan's hunches so often turn out to be right ! He has never fancied the idea of *borealis* and *garei* being subspecies of the same species.



Figs. 9–10.—Distribution of the fringing forms of *Clethrionomys glareolus* Schreber and *Microtus agrestis* L. After Zimmerman, 1950.

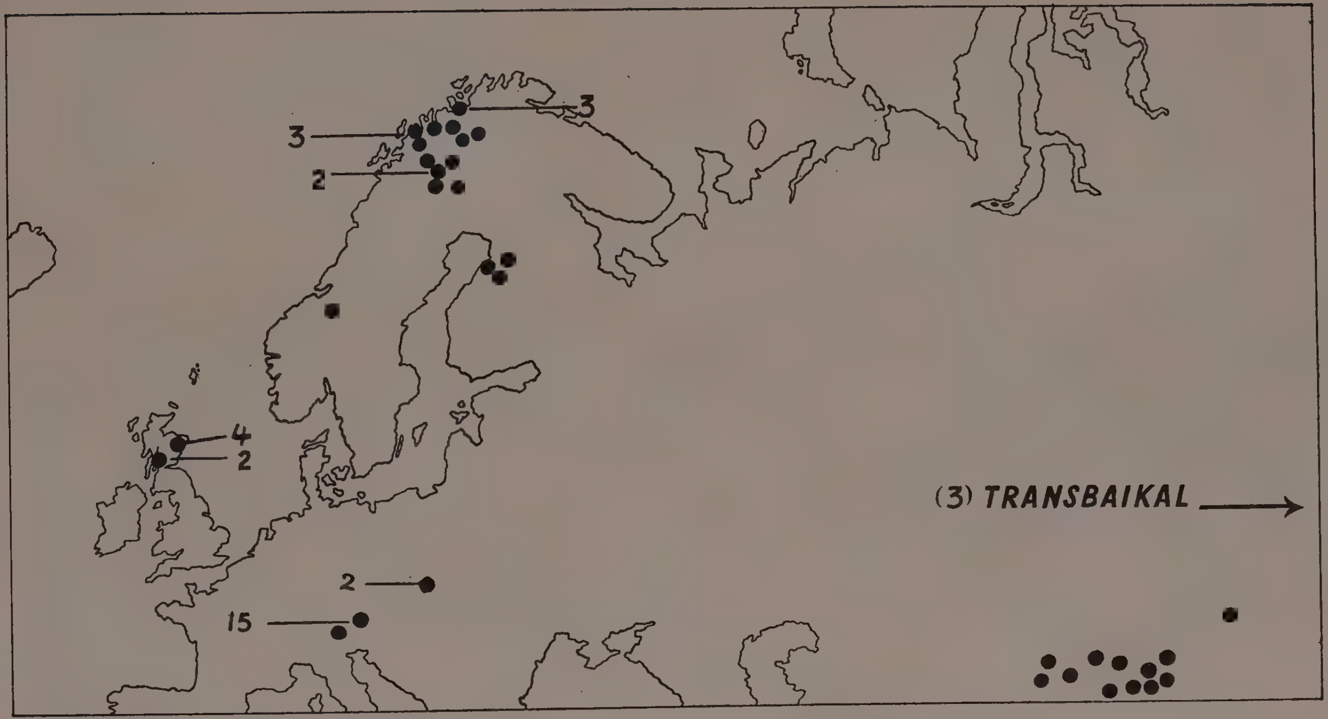


FIG. 11.—Distribution of *Megabothris rectangulatus* Wahlg. The circles represent single records unless accompanied by a figure (figures refer to the number of records from each locality).

Peus (1954), however, does not think it likely that the process of displacement by *garei* is still in progress. He prefers the idea that passive spread and reintroduction of *C. borealis* on migrating birds account for the overlap of the two species where they occur. Williamson (letter of 24th April, 1954) also thinks it likely that the occurrences of *C. borealis* on the mainland are not relict but due to re-invasion. Owing to the fact that no physiological barrier to interbreeding with *C. garei* has been developed, it is unable to consolidate its secondary colonisation of the mainland in the Wheatear niche. There is another point of interest to which he has drawn my attention. We have found (details to be published elsewhere) that bird fleas on Fair Isle are apparently more active in the spring,[13] and that trapped migrants chiefly harbour *C. borealis* at that season. (*C. borealis* has been taken from only one autumn migrant (see p. 298)). It is therefore the spring migrants which are the chief agents in dispersal. He points out that practically all the Fair Isle spring migrants are either birds on their way northwards to breed in Iceland, Faröe or Greenland, or species which get a westward drift from the Skagerrak in easterly weather after travelling north-westwards through central Europe from Italy or even further east. It is therefore possible for these birds to carry *C. borealis* annually north-westwards (in the case of the direct migration) or north-eastwards (in the case of re-orientated drift-migrants) from the western fringe of Europe.

These discussions are interesting, but of course purely speculative. For instance, we know little or nothing of the distribution of *C. garei* in Switzerland (a key area), but it appears to be a very scarce flea or absent in that country even at low altitudes. Nor do we understand the temperature and humidity requirements of the larvae of either species ; this factor may play a very important part in the distribution of *C. borealis*.

Are there other cases of fringing distributions among fleas? This is a question which can only be answered by further collecting. For instance, in 1950 Zimmermann published distribution maps of five fringing forms of the central European voles. In figs. 9, 10 and 11 the distribution of the fringing forms of *Microtus agrestis* L. and *Clethrionomys glareolus* Schreber and that of *Megabothris rectangulatus* Wahlg. are compared, and it will be seen that they have a great deal in common. But the distribution of *M. rectangulatus*[14] may be purely a boreo-Alpine type, although this is rather unlikely. It would be extremely interesting, for instance, if further collecting established the presence of *M. rectangulatus* in the Channel Isles, since this would provide very good evidence that it is linked to the fringing forms of voles. Its relationship with other vole fleas such as *M. turbidus* and *M. walkeri* is also well worth investigation.

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[13] Before Williamson and myself began this study of fleas from migrants Dr. Jordan had an idea that we should find this to be so. " The fleas breed in the nests, going on breeding after the birds' breeding season, and hibernate. In spring they pounce on the returning migrants, and have a first meal of blood . . . some fleas may leave the birds, others may be carried along to the nesting-place (and so on) over the whole area over which the migrants disperse ". (Letter of 22nd September, 1947.)

[14] For list of hosts see annotations to the references.

References.

* Papers containing records of *C. borealis* are marked *.
† Papers containing records of *M. rectangulatus* are marked †.

†Allan, R. M., [1953, Personal communication.] Four records of *M. rectangulatus* from the Bank Vole (1), Water Vole (2) and Stoat (1) from Aberdeenshire, Scotland.

Beirne, B. P., 1952, *The Origin and History of the British Fauna.* London. Pp. 1–164, 60 maps.

†Beklemisheva, V. N., and Ioff, I., 1949, *Aphaniptera of Kirgizia (U.S.S.R.). Ectoparasites, Fauna, Ecology and epidemiological significance.* First Edn. 1949. Academy of Medical Sciences of U.S.S.R. [Translation received from Colonel Traub. Records of *M. rectangulus :*

" The flea of forest rodents particularly red-haired *Microtus* genus *Clethrionomys* (*Evotomys*) variety but often found on many rodents living in the neighbourhood of fam. Muridae, Cricetidae, Sciuridae, also on small carnivores.

" Dist. . . . as far east as Altai and Transbaikal and penetrates to Tian-Shan together with other elements of northern forest fauna."]

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*Hale Carpenter, G. D., 1938, Notes on insects collected in West Greenland by the Oxford University Greenland Expedition, 1936. *Ann. Mag. nat. Hist.* (11) **1** : 529–553. (*See* p. 553.)

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†——, [1954, Personal communication.] *M. rectangulatus* from *Clethrionomys glareolus* from Ober Gurgl, Tyrol, Austria, collected by J. R. Vockeroth, 28.vii.53. Specimen in the Canadian National Collection.

†Hopkins, G. H. E., [1953, Personal communication.] Records of *M. rectangulatus* (4 females) from *Microtus gregalis* collected by G. A. Burney at Malta, Irkutsk, and 2 males and 3 females (determinations checked by K. Jordan) from Muridae from Chilik Mountains, Tien-Shan, sent by I. Ioff. (All in the British Museum C. Rothschild collection.)

†Ioff, I., 1928, Über neue Aphanipteren in der Sammlung des Zoologischen Museums der Akademie der Wissenschaften. *Annu. Mus. zool. Acad. Sci. St. Petersb.* **28** : 407–439, 20 figs. [Record of one male as *C. baikalensis* (= *M. rectangulatus*) from *Evotomys rufocanus* Transbaikalien, Balsino, Bezirk Tschita (p. 416).]

*——, 1936, Zur Systematik der Flöhe aus der Unterfamilie Ceratophyllinae. *Z. Parasitenk.* **9** : 73–124, figs. 1–73. [Figure of the spermatheca of *C. borealis* " from Kaukasus "—no description (p. 120, fig. 63).]

Ioff, I., 1941, The ecology of fleas in connection with their epidemiological importance. [In Russian.] *Pyatigorsk. Ordzhonik. kraev. Izd.* 116 pp. 9 figs., 1 chart.

†Jordan, K., 1932, The Siphonaptera collected by Mr. J. L. C. Musters in Norway on the Lemming. *Novit. zool.* **38** : 256–257, 2 figs. [*M. rectangulatus* from *Lemmus lemmus*.]

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APPENDIX.

Since sending this paper to press, Colonel Robert Traub has kindly sent me the translation of a Russian paper by N. F. Darskaya (1950 : Key to the bird-fleas of the genus *Ceratophyllus. Mater. K. Poznan. Faun. Flor. S.S.S.R., Ectoparasites,* N.S., 2 : (*Zool. Sect.*) 85–105, figs. 1–19). The following new records of *C. borealis* are given on page one : " The Karelian isthmus (Khallila) ; besides this it is found . . . in Caucasus, around the town of Dzaudzhikau (Redant), near the sources of the Kuban river (Uchkulan), and in mountainous Azerbaidjan (Isti-Su in the Kelbadzhar region). It has been found chiefly in ground nests of birds—gulls, fulmars, various passerine birds, etc.—less often in nests in trees ; once it was found (three females and one male) with *C. gallinae* on starlings (Khallila)." She also records *Ceratophyllus garei* : " From the Velova forest, from the Murmansk coast, from Leningrad, Vologda and Molotov areas, from Ural (Sob river), from western Siberia (Kondo-Sosva reservation), from the Lena river (Ust–Kut), from the delta of the Kolyma river (Pokhodskoe village), from the Maritime area (Suputin reservation, Lesozavodsk, Lazo region, Khasan region)."

She describes a new species, *Ceratophyllus frigoris*, morphologically very close to *garei*, which she surmises replaces this species in the Caucasus : " Twenty-three females and twenty-seven males found in nests of *Phoenicurus ochrurus* and *Anthus spinoletta* on the Caucasus range (Cross pass) . . . also seventeen females and fifteen males from nest of undetermined bird in Azerbaidjan (Isti-Su near Kelbadzhar.) . . . In both cases the fleas were collected in nests taken from cliffs in high mountain territory (more than 2000 m. above sea level)." From the drawings it appears to me that *C. frigoris* is very similar to, if not identical with, the intermediates between *C. borealis* and *C. garei* described in my paper above.

Received 30th March, 1954.

SIPHONAPTERA FROM BARILOCHE, ARGENTINA, COLLECTED BY DR. J. M. DE LA BARRERA IN 1952–1954.

By F. G. A. M. SMIT
(*British Museum* (*Natural History*), *The Zoological Museum, Tring, Herts.*)

With 24 Text-figures.

SINCE 1900 the growth of our knowledge of fleas has paralleled that of human plague and wild-rodent plague, for the discovery that fleas are the main vectors of the disease gave an impetus to the taxonomic studies of these insects. In 1897, the year of publication of Ogata's paper in which for the first time the suggestion was made that plague might be transmitted by rat-fleas, the number of described fleas was 68. Since then, up till the end of 1954, no less than 1386 species and subspecies have been described, making a total of 1454 (synonyms are excluded from these figures). The gradual increase in the number of described fleas can be seen from fig. 1 ; this chart indicates that many fleas still remain to be discovered. Of the 1454 fleas known to science, 640 were described by the Hon. N. C. Rothschild and Dr. K. Jordan (200 by Rothschild, 192 by Jordan and Rothschild, 248 by Jordan). The results of these intensive studies in flea-taxonomy proved of great value to workers investigating plague. Studies on plague continue, especially with relation to its epidemiology, and fleas collected during rodent-flea surveys are still being sent to specialists for identification ; plague investigators thus continue to contribute vastly to taxonomic and faunistic knowledge of fleas. One of the most prolific collectors of fleas to-day is Dr. J. M. de la Barrera, who studies wild-rodent plague in South America. Material received from Dr. de la Barrera has already formed the basis for three papers by Dr. Jordan, in which 16 species and subspecies are described as new, and many new facts are published concerning hosts and distribution of known fleas (1939, *Novit. zool.* **41** : 292–303 ; 1942, *Rev. Inst. Bact.* **10** : 401–460 ; 1953, *Bull. Brit. Mus.* (*Nat. Hist.*), (*Ent.*) **3** : 179–186). The last of these three papers deals with " a most remarkable flea "[1], viz. *Barreropsylla excelsa*, which was part of a fine collection made in 1952 by Dr. de la Barrera near San Carlos de Bariloche, Rio Negro, Argentina. Dr. Jordan recently invited me to deal with the other species contained in this Bariloche collection, together with further material from the Bariloche district collected by the donor in 1953 and 1954. Two new species (one new *Ctenoparia*, and one new *Tetrapsyllus*) are here described, and also the hitherto unknown male of *Sphinctopsylla ares* and the female of *Ectinorus onychius onychius* ; of the nine known species in this collection, seven were thus far only known from type-material. The Bariloche collection here dealt with is therefore of great value and we owe Dr. de la Barrera a debt of profound gratitude for further enhancing our knowledge of the South American flea fauna.

All specimens were collected by Dr. J. M. de la Barrera at San Pedro on the south shore of lake Nahuel Huapi, Rio Negro Territory ; San Pedro is situated at 810 meters above sea-level at a distance of 21 km. W.N.W. from the town of San Carlos de Bariloche. Most of the material has been presented by the collector to the British Museum (Natural History); it has been incorporated in the museum's collection of fleas at Tring.

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[1] Dr. Jordan's description of this flea inspired the third leader in *The Times* of 6th January, 1954, where his paper is referred to as " an entomological panegyric in praise of a flea."

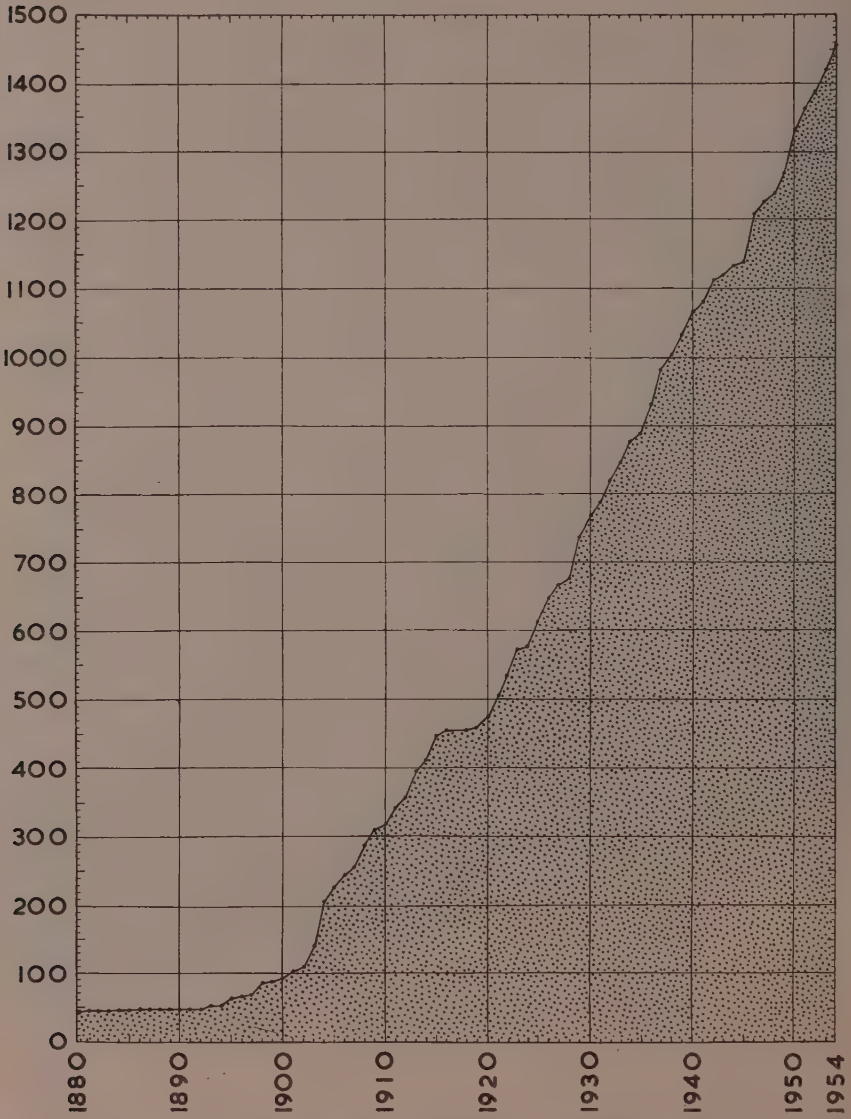


Fig. 1.—Chart showing the number of species and subspecies of fleas described between the end of 1880 (43) and the end of 1954 (1454). Synonyms are excluded.

Family Stephanocircidae.

Barreropsylla excelsa Jordan, 1953.

The description of this intriguing "Incredible Flea" was based on 1 ♂ (holotype) and 1 ♀ (allotype), *ex Akodon* sp., 3.vii.1952. One additional pair has since been received: 1 ♂, *ex Euneomys dabbenei*, 9.vii.1953, 1 ♀ *ex Akodon neocenus*, 19.vii.1953. Both *Akodon* and *Euneomys* belong to the rodent-family Cricetidae.

Plocopsylla wolffsohni (Rothschild), 1909.

Ex Akodon sp.: 1 ♂, 3.vii.1952; *ex Akodon nucus*: 3 ♂ 2 ♀, 14 and 16.vii. 1953; *ex Akodon neocenus*: 3 ♀, 19.vii.1953; *ex Irenomys* sp.: 1 ♂ 1 ♀, 3 and 10.vii.1952; *ex Abrothrix hirta modestior*: 1 ♂ 1 ♀, 3 and 5.vii.1952; 1 ♂ 1 ♀, 9.vii.1953; *ex Oryzomys longicaudatus*: 2 ♂ 1 ♀, 8 and 14.vii.1952; 1 ♂ 2 ♀, 12.vii.1953; *ex Euneomys dabbenei*: 1 ♀, 8.vii.1952; 1 ♂ 3 ♀, 9.vii. 1953; *ex Notiomys valdivianus fossor*: 5 ♀, 7 and 15.vii.1953.

This species was hitherto only known from two males and three females from Valparaiso, Chile (*ex Akodon olivaceus*, *A. longipilis*, *Phyllotis darwini* and *Marmosa elegans*), and apparently had not been collected since 1909. There appear to be a few slight differences in the male genitalia between the Chilean specimens and those recorded above, but not until more material from Valparaiso comes to hand can these differences be rightly evaluated.

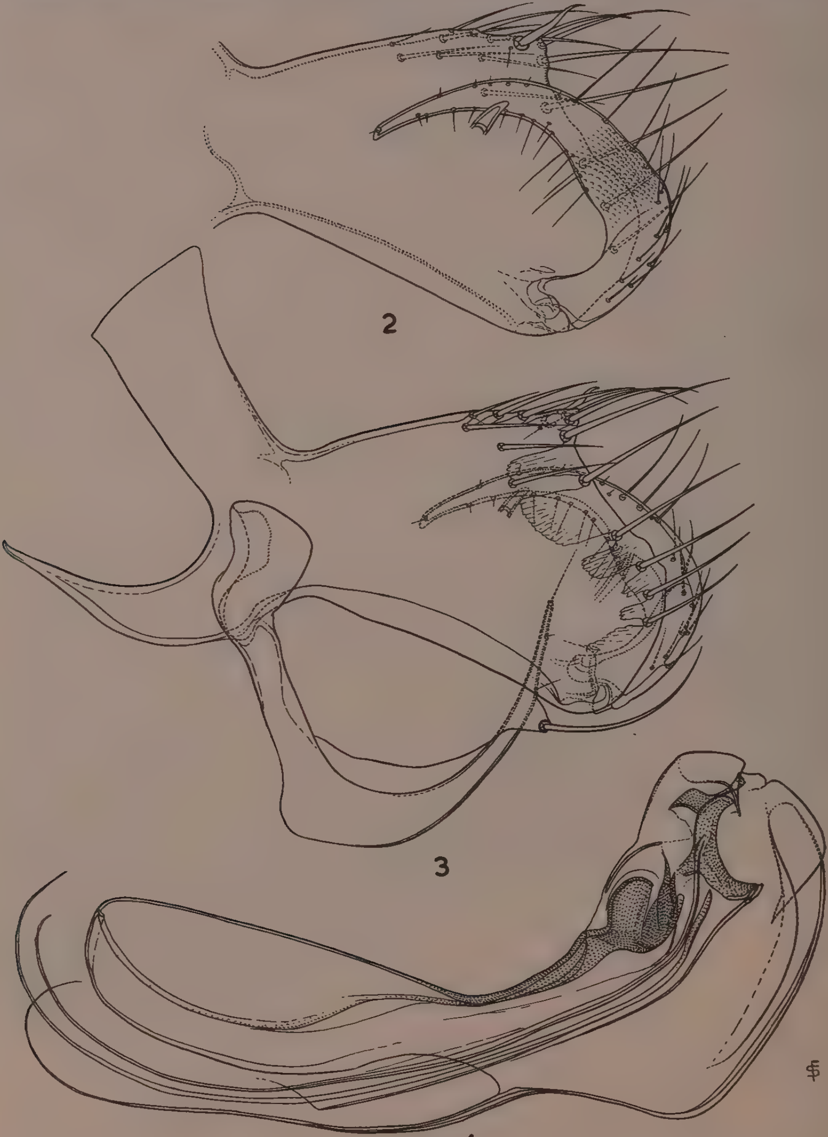
Sphinctopsylla ares (Rothschild), 1911. (Figs. 2–5.)

Ex Abrothrix hirta modestior: 1 ♀, 5.vii.1952; 1 ♂ 2 ♀, 9.vii.1953; *ex Akodon* sp.: 1 ♀, 7.vii.1952; *ex Akodon nucus*: 3 ♀, 7.vii.1953; *ex Akodon neocenus*: 2 ♀, 8 and 12.vii.1953; *ex Oryzomys longicaudatus*: 3 ♀, 8, 12 and 14.vii.1952; 1 ♂, 12.vii.1953; 3 ♂ 5 ♀, 25 and 26.ii.1954; *ex Notiomys valdivianus fossor*: 2 ♀, 9.vii.1953; *ex Rattus* sp.: 2 ♀, 12.vii.1952.

It is most gratifying that Dr. de la Barrera succeeded in collecting such a nice series of this species, which hitherto was only known from the female holotype from Temuco, Chile, *ex Akodon olivaceus*. The male is here described, and the variation in the numbers of ctenidial spines and of the tergal spinelets in the female is also given (in these counts the female holotype is also included).

Male.—Helmet ctenidium consists of 14–16 spines and in only one of the five available males are the numbers on each side of the head the same (15/15; in the other four specimens the numbers are: 14/15, 14/15, 15/16, 15/16). In the female the helmet ctenidium has 16 or 17 spines and in only three of the 14 females are the numbers on each side of the head unequal. Both sexes have a genal ctenidium of five spines. Pronotum with three well-developed rows of setae in both sexes. Pronotal ctenidium consists of 23–26 spines in the male; 26 appears to be the usual number (three males have 26 spines in this ctenidium, one male 23, the other 24); in the female the number of pronotal spines varies from 26–28. The numbers of marginal spinelets on one side of terga I–VI in the male are: 3–4 (sometimes 2), 3–4, 3–5, 3–4 (seldom 5), 2–3, 1 (seldom 0); for the female the numbers are: 3–4, 3–6, 3–5, 2–4, 1–2 (rarely 3 or 4), 0 (occasionally 1 or 2). Of the two antesensilial setae in the male only the upper is well-developed, the lower being reduced to a minute seta, as is normal in males of all the species of the genus. The sensilium has only 13 trichobothria each side in both sexes, as in the other species of the genus; 13 trichobothria on each side of the sensilium is the rule in the whole family Stephanocircidae, with only a few exceptions in which the number is 14 or 15.

Modified abdominal segments of male (figs. 2–5).—Tergum VIII large and extending far downward, with only one seta, which is situated below the spiracular fossa. Sternum VIII strongly modified, consisting of a narrow and bent proximal arm, which forks behind the



Figs. 2–4.—*Sphinctopsylla ares* (Rothschild) (from Bariloche). (2) Inner aspect of clasper. (3) Clasper and sternum IX. (4) Phallosome.

proximal arm of sternum IX into a dorsal membranous spiculose lobe and a long ventral distal arm, which is narrow in its basal half and forms a median ventral cone bearing one large curved seta, while its apical portion is dilated and membranous and finely striated at its dorso-apical angle. Apodeme of tergum IX fairly narrow; the upwards curved manubrium basally broad but tapers to a very narrow apex. Corpus of clasper large, twice as broad apically as basally; with several longish setae on the preapical part of the dorsal margin, 5–7 fairly long setae along its posterior margin and one slightly sigmoid curved spiniform seta preapically near the dorso-apical angle on the inner surface. Movable process strongly curved, sickle-shaped, with a number of setae along the posterior margin, the ones on the lower half being placed on the inner surface of the process, which is in its middle part rugulose owing to the formation of cuticular scale-like rounded teeth. A relatively long "catch"[2] on the inner side of the corpus of the clasper keeps the movable process in position when not in use; this structure, which seems to be peculiar to the

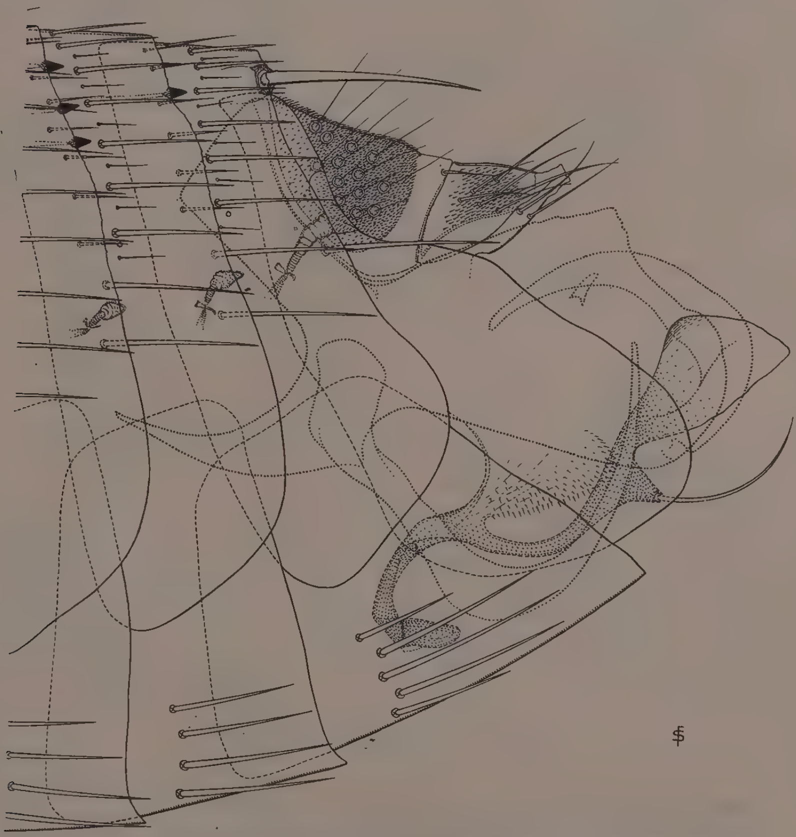


Fig. 5.—*Sphinctopsylla ares* (Rothschild) (from Bariloche). Modified abdominal segments of male (clasper and sternum IX in dotted lines).

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[2] The "lateral projection of the clasper" of Hopkins and Rothschild (*Catalogue of the Rothschild Collection of Fleas*, Vol. 2).

Craneopsyllinae, may be termed the *pessulus*. Sternum IX with a long and narrow distal arm, tapering towards its apex which bears one slender seta ; preapically this arm bears two small setae on the ventral margin. Anal tergum densely spiculose. For the structure of the phallosome see fig. 4.

Remarks.—Although *Sphinctopsylla ares* agrees with *S. tolmera* Jordan, 1931, as regards the presence of three rows of setae on the pronotum and numerous spicules on the anal tergum of the male, in the structure of the male genitalia *S. ares* proves to be more closely related to *S. inca* (Rothschild), 1914. The latter species usually has the first of the three pronotal rows incomplete and in most of the males the anal tergum is not spiculose, although in a few specimens several spicules are present and exceptionally the tergum may even be densely spiculose.

Family HYSTRICHOPSYLLIDAE.

Agastopsylla boxi Jordan and Rothschild, 1923.

Ex Notiomys valdivianus fossor : 1 ♂ 1 ♀, 9 and 15.vii.1953.

This species was only known from the type material (1 ♂, 2 ♀), which was collected in the Chubut Territory, Argentina (Leleque and Cholila, *ex Abrothrix suffusus* and *Ctenomys haigi*).

Chiliopsylla allophyla (Rothschild), 1908.

Ex Oryzomys longicaudatus : 1 ♀, 25.ii.1954.

This flea was hitherto only known from Chile (Temuco and Valdivia, *ex Dromiciops australis*).

Neotyphloceras crassispina crassispina Rothschild, 1914.

Ex Abrothrix hirta modestior : 1 ♀, 3.vii.1952 ; *ex Notiomys valdivianus fossor* : 1 ♀, 9.vii.1953 ; *ex Oryzomys longicaudatus* : 1 ♀, 14.vii.1952 ; 2 ♂, 1 ♀, 25 and 26.ii.1954 ; *ex Rattus* sp. : 3 ♂, 6 and 12.vii.1952.

The occurrence of this subspecies so far south is most unexpected, for it was only known from Peru (Pachacayo, Matucana, San Ignacio, Caylloma and Caccachara ; *ex Phyllotis amicus*, *P. arenarius*, *Abrocoma* sp., *Auliscomys boliviensis*, *Chinchillula sahamae* and *Chroeomys pulcherrimus*) ; in the low-lands southwest of the Andes range (Valparaiso and San Cristobal, Chile) subspecies *chilensis* Jordan, 1936, occurs, and from east of the Andes (" Otro Cerro" , Prov. of Rioja ; Pilcañeu, Rio Negro ; Piedra Pintada, Terr. of Neuquen—all in Argentina—and in the Dept. of Potosi, Bolivia) subspecies *hemisus* Jordan, 1936, has been reported.

Ctenoparia jordani sp. n. (Figs. 6–14)

Male holotype *ex Oryzomys longicaudatus*, 12.vii.1953 ; female allotype *ex Akodon* sp., 3.vii.1952. Paratypes : *ex Akodon* sp. : 1 ♂, 1 ♀, 7 and 10.vii.1952; *ex Akodon nucus* : 2 ♀, 7 and 11.vii.1953 ; *ex Abrothrix hirta modestior* : 2 ♀, 9.vii.1953 ; *ex Notiomys valdivianus fossor*, 2 ♂, 1 ♀, 7, 9 and 20.vii.1953 ; *ex Oryzomys longicaudatus* : 1 ♂, 12.vii.1953 ; *ex Rattus* sp. : 3 ♀, 6.vii.1952.

The new species is easily distinguished from the only other known species of the genus, *C. inopinata* Rothschild, 1909 (of which only the female is known), by the absence of a ctenidium on abdominal tergum II, the presence of one marginal spinelet near the dorsum of terga II–IV (none in *C. inopinata*) and by the genal ctenidium having seven long and sharply pointed spines instead of eight shorter and blunter spines. Other marked differences from *C. inopinata* are: an incomplete first row of setae on the postantennal region of the head; the genal process is concealed by the last spine of the genal ctenidium; the spines of the pronotal ctenidium are longer than half the length of the pronotum,

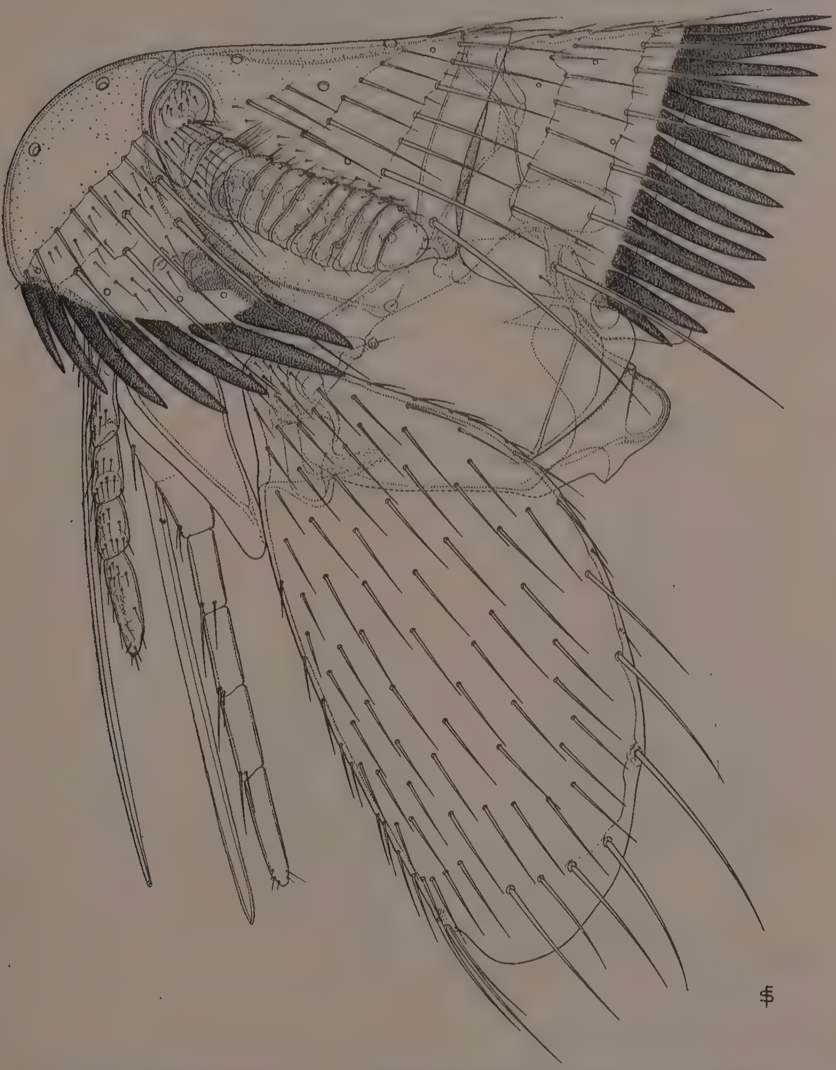
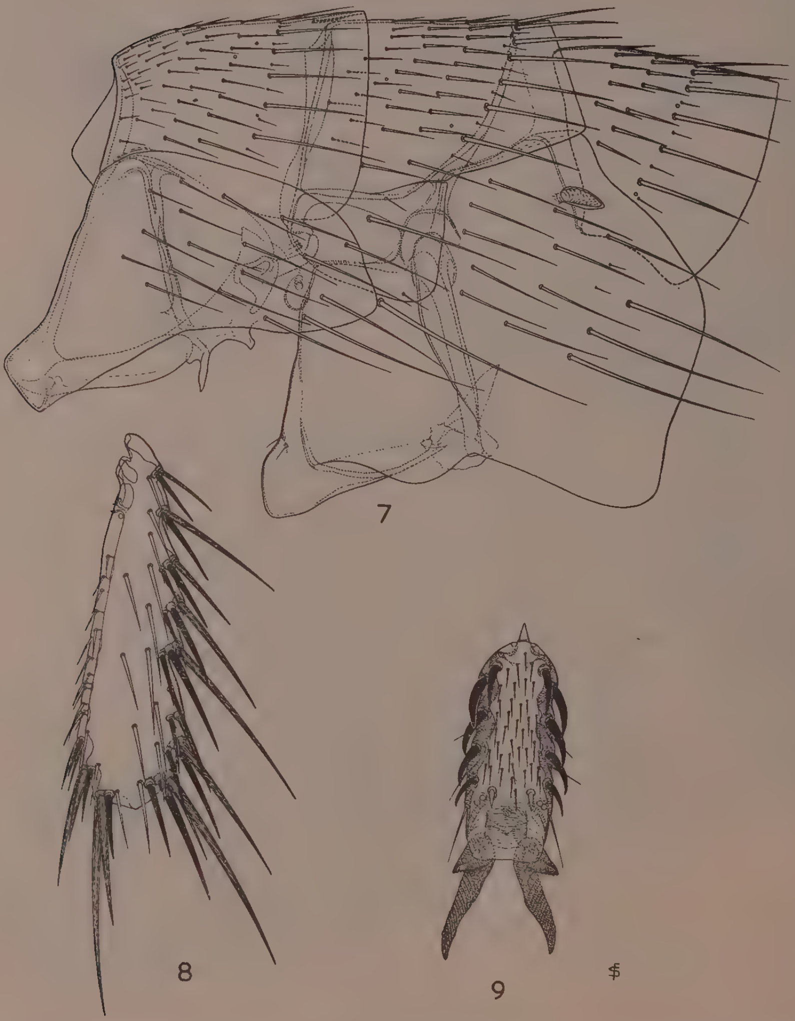


FIG. 6.—*Ctenoparia jordani* sp. n. Head, prothorax and fore coxa of male (paratype).

instead of shorter; the spiniform setae along the posterior margin of the tibiae do not form a false comb; two antesensilial setae in both sexes instead of three; sternum VII of female without a ventral sinus.



Figs. 7–9.—*Ctenoparia jordani* sp. n. (7) Mesothorax, metathorax and tergum I of male (paratype). (8) Hind tibia of female (paratype). (9) Last hind tarsal segment of female (paratype).

Head[3] (fig. 6).—Fronto-clypeal margin strongly and smoothly rounded, without an angle or tubercle. Preoral tuber concealed by the bases of the first two genal spines. First (anterior) row on preantennal part of head usually with 7–8 setae (varying from 5–10), second preantennal row with three long setae (in one male there are two irregularly placed additional setae), and the third (ocular) row consists of two long setae, the upper of which is placed above the eye near the anterior margin of the antennal fossa. A number of microsetae scattered in between these rows but not below or behind the eye. Genal ctenidium along the whole of the genal margin; it consists of seven (in one male on one side eight slightly curved (except for the hindermost two, which are practically straight) long and sharply pointed spines. Genal process not visible. Eye reduced, semi-oval. Maxillary palps short, not quite reaching to the middle of the anterior margin of the fore coxa. Stipes of the usual triangular shape. Lacinia with finely serrate margins, its apex reaching beyond those of epipharynx and labial palps (this is unusual, for the apices of these three mouthparts normally lie on the same level). Labial palp consisting of five segments, its apex reaching to about four-fifths of the anterior margin of the fore coxa. The labrum is hidden by the spines of the genal ctenidium and therefore invisible. Antenna: scapus with a number of microsetae on its basal part and halfway a row of thin setae which do not reach beyond its apical margin; pedicellus with a row of thin setae, several of which reach a little beyond its apical margin, and a tuft of thin setae at its posterior margin in the male, in the female this tuft is smaller owing to the shorter posterior margin of the pedicellus; clava distinctly nine-segmented and long in both sexes, although in the female the clava is a little shorter than that of the male. Antennal fossa dorsally bordered by a row of 14–16 small setae in the male, 10–17 in the female. Anterior part of the tentorium distinct in front of the eye, where it is inserted into the cranial wall; the whole of the tentorial rod can be seen in fig. 6. Interantennal suture very distinct in both sexes. Postantennal region of head with three rows of setae; the first row with three (occasionally 2 or 4) setae, the second row with 7 or 8 (sometimes 6) and the posterior row with 7 or 8 setae. One additional long seta near the ventro-posterior angle of the postantennal region. Occipital groove in the male not very deep.

Thorax (figs. 6 and 7).—Pronotum with two rows of setae, the first row containing 7–10 setae, the second 7 in the male (occasionally 8) and 8 in the female. Pronotal ctenidium consisting of 28–30 spines on both sides together; the spines are about four-fifths the length of the pronotum. Mesonotum with three distinct rows of setae and a number of irregularly placed small setae in front of the first row; the first and second row each with 8–11 setae, the third with 6–7 setae. Under the collar of the mesonotum, near the dorsum, one long pseudoseta each side in both sexes. Mesopleurum with 14–17 setae in the male, 17–20 in the female. Mesopleural rod dorsally forked with the prongs running parallel and close to each other. Metanotum with three distinct rows of setae, anterior to which there are a number of setae which may or may not be partially arranged to form one or two short rows; the first and second of the three distinct rows contain 8–11 setae, the third 6 or 7 in the male, 6 in the female. Metapleural arch well developed, as are also the pleural rod and ridge. Metepisternum with one long seta, below which one or two shorter ones. Metasternum with one long seta and obliquely above this a minute one. Metepimeron with 12–17 irregularly placed setae in the male, 14–19 in the female; if the posterior setae form a row, then there may be intercalary setae between several pairs of the main setae. Squamulum of metasternum shaped as a thick rounded knob.

Legs.—Fore coxa setose over the whole of its outer surface, mid and hind coxa with a number of setae at and near the anterior margin; hind coxa without spiniform setae on its inner surface, but with rather few short setae near the basal anterior part of this surface. Posterior margin of fore tibia with six notches, containing 2, 2, 3, 3, 3 and 3 setae respectively; posterior margin of mid tibia with seven notches, containing 2, 2, 3, 3, 3, 3 and 3 setae; posterior margin of hind tibia with eight notches, containing 2, 2, 3, 3, 3, 2, 3 and 3

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[3] Counts of setae relate only to one side of the body and apply to both sexes, unless stated otherwise.

setae from base to apex (fig. 8). Fifth segment of all tarsi with five pairs of lateral setae, the first (basal) pair displaced a little on to the plantar surface ; the latter bears numerous minute setae. Two very short preapical plantar setae ; the preapical lateral setae are also short. Tarsal claws of normal shape and with the usual serration (fig. 9).

Abdomen.—Terga I–IV bear in the male three rows of setae, terga V–VII only two (there may be one or two setae in front of the anterior row on terga V and VI, but this is not normal) ; in the female each of these seven terga has three rows. The numbers of setae in these rows on terga I–VII in the male are respectively : T.I : 4–6, 7–8, 6 ; T.II : 4–6, 10–12, 9–11 ; T.III : 2–3, 9–11, 9–11 ; T.IV : 1–3, 9–11, 9–11 ; T.V : 8–9, 9–10 ;

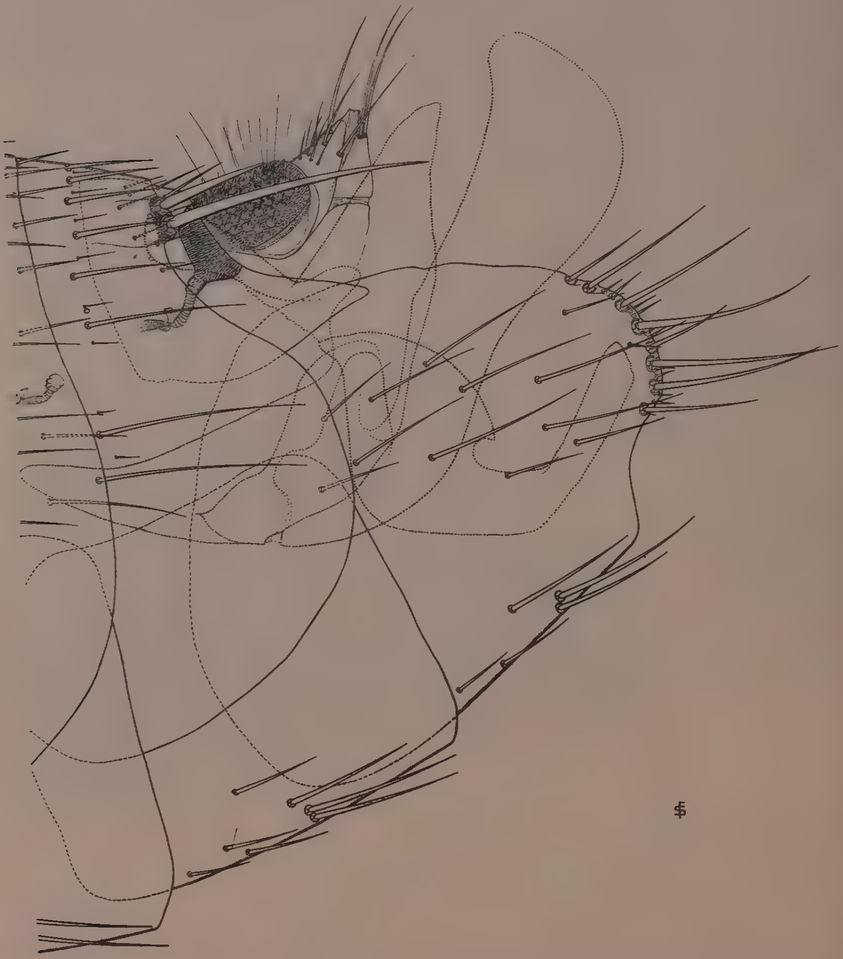
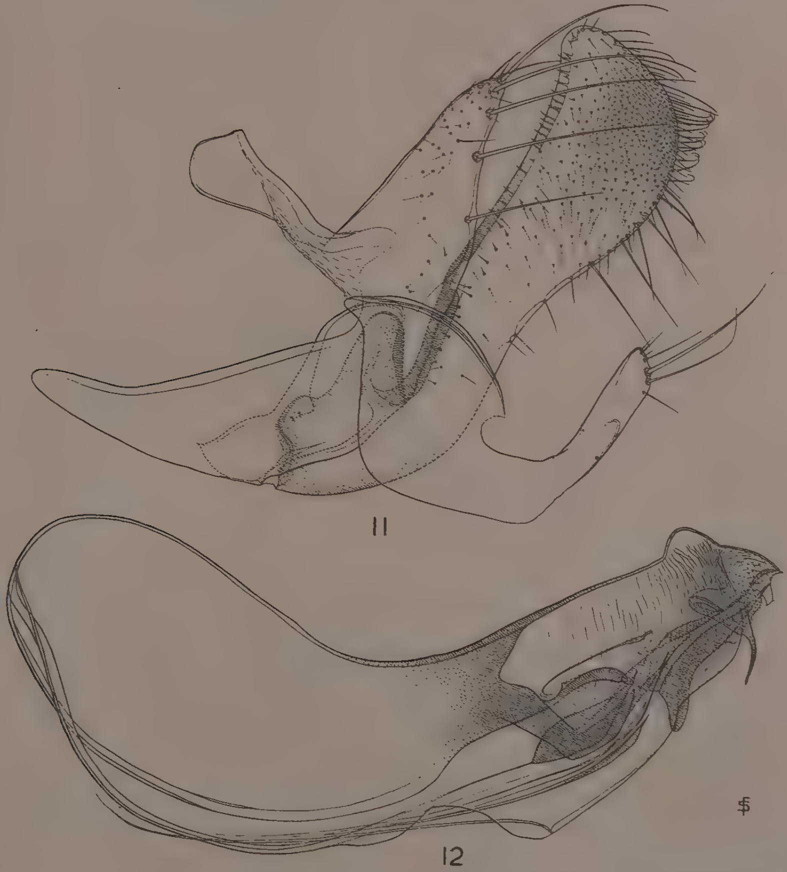


Fig. 10.—*Ctenoparia jordani* sp. n. Modified abdominal segments of male, holotype (clasper and sternum IX in dotted lines).

T.VI : 7–8, 9–10 ; T.VII : 7–8, 8–9 ; in the female the numbers are T.I : 6–8, 7–10, 5–6 ; T.II : 5–8, 11–15, 10–12 ; T.III : 3–6, 11–12, 10–12 ; T.IV : 1–4, 10–12, 10–11 ; T.V : 1–3 ; 9–10, 9–10 ; T.VI : 2–3, 7–10, 8–9 ; T.VII : 2–6, 7–9, 6–7. Terga II–IV bear one stout marginal subdorsal spinelet on each side, but one or both may be absent on tergum IV in the female. Tergum VII with two antesensilial setae in both sexes ; in the male the upper seta is one-third to two-fifths the length of the lower, in the female the upper seta is about half the length of the lower. Sterna II–VII in both sexes with one main row, in front of which is a group of setae, several of which may form a short row ; in the numbers of setae given here, the first is that of the group of setae before the main row, the latter being the second number. Male : St.II : 0–1, 1 ; St.III : 2–3, 4–5 ; St.IV : 1–2, 4–5 ; St.V : 2, 4–5 ; St. VI : 2–3, 4 ; St. VII : 2–4, 4. Female : St.II : 2–3, 2–3 ; St. III : 3–7, 5–7 ; St.IV : 3–7, 4–6 ; St. V : 4–6, 5–6 ; St.VI : 3–7, 4–6 ; St.VII : 12–17 (the setae of St.VII in the female are very irregularly arranged and it would be difficult to assess the exact number of setae in the main row of this sternum, hence the numbers 12–17 are those of all



FIGS. 11–12.—*Ctenoparia jordani* sp. n. (11) Clasper and sternum IX (holotype). (12) Phallosome (holotype).

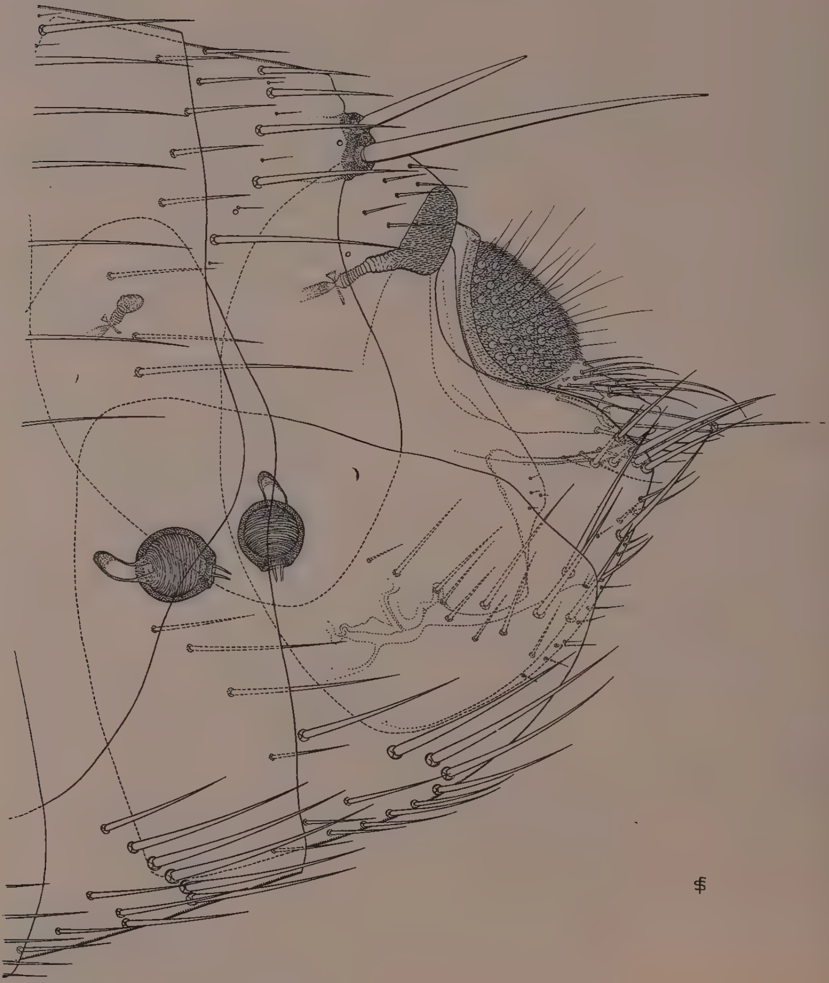


FIG. 13.—*Ctenoparia jordani* sp. n. Terminal segments of female (allotype).

setae together on one side of St. VII). The posterior margin of St. VII of the female forms a very broad lobe, but there is little indication where the ventral and posterior margins meet (fig. 13).

Modified abdominal segments, male (figs. 10 and 11).—Tergum VIII relatively small, its ventro-apical angle drawn out into a triangular lobe; anterior to the fairly large spiracular fossa a group of 5–10 short setae, but no such setae below the fossa. Sternum VIII very large, its posterior margin forming a broad rounded lobe which bears a row of seven to nine long setae and 5–10 small ones; along the ventral margin four to seven setae and on its lateral surface 9–14 widely spaced long setae. Apodeme of tergum IX rather small and only its dorsal part sclerotised, the connection with the manubrium being membranous.

Fixed process of clasper triangular, with five long and slender setae along its posterior margin, several shorter ones at the apex and a number of thin and short setae scattered over the inner side of the process. Manubrium basally broad, but tapering towards the apex. Movable process of clasper very large, its apical half posteriorly expanded, where it bears numerous setae along the margin; the inner surface of this process is covered (except for the basal portion) with numerous thin setae. The acetabular part of the movable process is also large and the acetabulum is modified to receive the acetabular part; it is curious that the acetabulum thus occupies the basal half of the manubrium. Proximal arm of sternum IX very broad, with a rounded dorsal margin, the anterior margin of this arm bent to form a right angle. Distal arm of sternum IX rather narrow, with two or three long slender setae and several shorter ones at the oblique apical margin. Sensilium dorsally straight, with over 30 trichobothria each side.

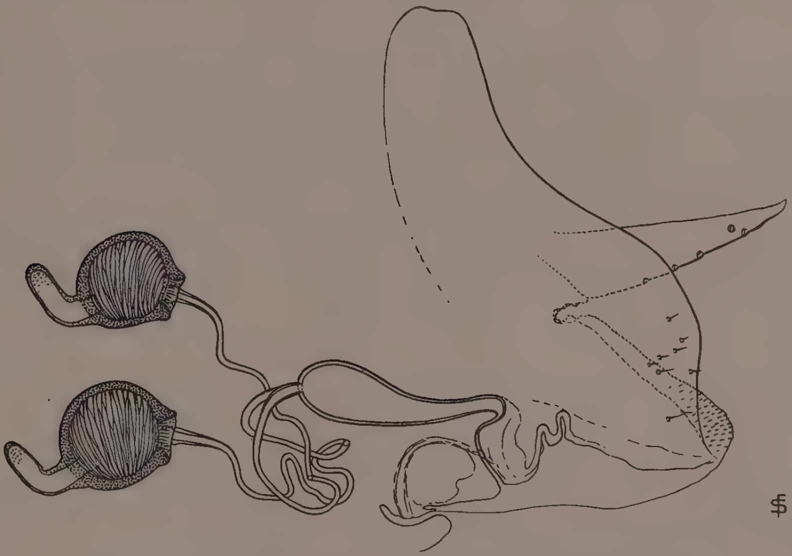


FIG. 14.—*Ctenoparia jordani* sp. n. Genitalia of female (paratype).

Phallosome (fig. 12).—Aedeagal apodeme very broad, with a rounded apex; tendons of phallosome short, not reaching the apex of the apodeme. Inner tube of aedeagus with a thick ventral wall. In three of the five males the apico-dorsal hump is less strongly convex than in the specimen shown in fig. 12.

Modified abdominal segments, female (figs. 13 and 14).—Tergum VIII with a fairly large spiracular fossa, similar to that of the male; anterior to this fossa a group of six to nine short setae. At the apico-ventral angle of tergum VIII three fairly long setae and on the inner surface three genital setae; along the ventral margin a number of mostly small setae and a very irregular row of long setae on the lower third of the lateral surface. Sternum VIII not much sclerotised, with two short apical setae. Sternum IX extending far upwards, its dorsal margin lying under the spiracular fossa of tergum VIII; with 4–8 minute setae near the posterior margin of its lower part. Sensilium dorsally fairly convex, with about 40 trichobothria each side. Anal tergum with a number of long and slender setae; anal stylet six or seven times as long as basally broad, with one apical seta, which is as long as the stylet, and two short preapical setae. Anal sternum with 4 or 5 ventral setae. The two spermathecae are of slightly unequal size (figs. 13, 14); the bulga of each spermatheca is globular and has a thick wall, the hilla is narrow and relatively short. Ductus bursae rather short, but the bursa copulatrix is long and club-shaped ; at the apex of the bursa the two ducti spermathecae are inserted.

Length : Male, 3–3½ mm. ; female, 3½–4 mm.

The new species described above is named after Dr. Karl Jordan as a token of profound gratitude for setting such a high standard and output of work throughout his life and which will be a continual inspiration to me.

As a result of the discovery of *Ctenoparia jordani*, it is necessary to give the following redescription of the genus *Ctenoparia* Rothschild.

Ctenoparia Rothschild, 1909.

Redescription.—Eye vestigial. With a genal ctenidium of seven or eight spines, extending over the whole length of the ventral margin of the preantennal part of the head. Labial palp five-segmented. Central tuber of head absent. Pleural arch of metathorax, and squamulum, well-developed. The stout setae along the posterior margin of the tibiae may or may not form a false comb. Oblique suture of the outer surface of mid coxa interrupted. Setae on first segment of hind tarsus short ; first segment of mid tarsus longer than the second. Fifth tarsal segment of all tarsi with five pairs of lateral setae, the basal pair of which may be shifted a little on to the plantar surface. With a developed ctenidium on tergum II or marginal spinelets on several terga.[4] Two or three antesensilial setae in both sexes. Sternum VIII of male large and not modified. Female with two spermathecae, and a long anal stylet at the lateral margin of the anal tergum. Neotropical.

Type species : *Ctenoparia inopinata* Rothschild, 1909.

Family RHOPALOPSYLLIDAE.

Tetrapsyllus tantillus (Jordan and Rothschild), 1923.

Tetrapsyllus litis Jordan, 1936, *Novit. zool.* **39** : 307. **Syn. nov.**

Ex Irenomys sp. : 1 ♂, 9.vii.1952 ; *ex Oryzomys longicaudatus* : 1 ♂, 1 ♀, 14.vii.1952 ; 1 ♀, 25.ii.1954 ; from nest of *Notiomys valdivianus fossor* : 1 ♀, 27.ii.1954 ; *ex Rattus* sp. : 1 ♂, 12.vii.1952 ; from nest of *Rattus norvegicus* : 1 ♂, 1 ♀, 20.ii.1954.

This species was described from five females from the Chubut Territory (Cholila and Leleque). The series recorded above, including both sexes, showed that the only known specimen (the male holotype) of *Tetrapsyllus litis* Jordan, 1936, (from Valparaiso, Chile) is not separable from males of *T. tantillus* and I therefore place *T. litis* Jordan, 1936, as a synonym of *T. tantillus* (Jordan and Rothschild), 1923. That Dr. Jordan should have considered *T. litis* to be distinct was inevitable, for having only one sex of *T. tantillus* he could not know that in this species the chaetotaxy is different in the two sexes : in the male the setae of the antennal pedicellus reach beyond the middle of the clava (but not to the apex), in the female beyond the apex ; in the male there is a short row of 2–4 setae each side in front of the main row on the pronotum, in the female there are only one or two dorsal setae representing the first row. Moreover, it is still the case that one would expect a specimen of *Tetrapsyllus* from Valparaiso to be different from one from the Chubut area, and on zoogeographical grounds I myself am surprised in being unable to detect any appreciable differences between the Chilean and Argentinean males.

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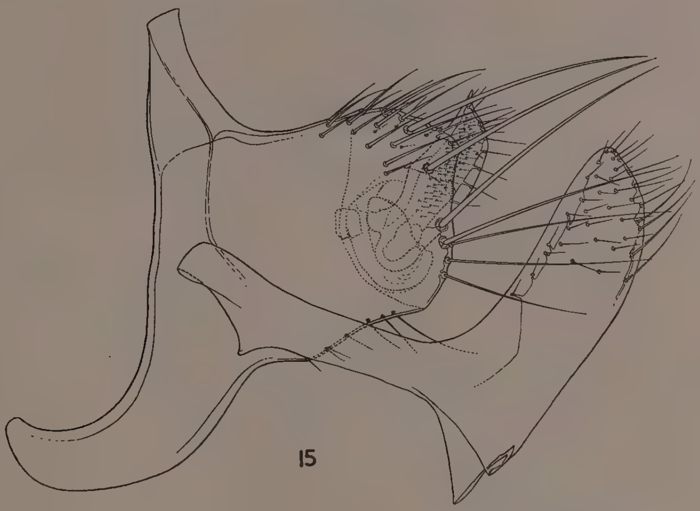
[4] Of the two known species, one has a developed ctenidium on tergum II and lacks spinelets on the remaining terga, while in the other the position is reversed, there being no ctenidium, but marginal spinelets are present on several terga.



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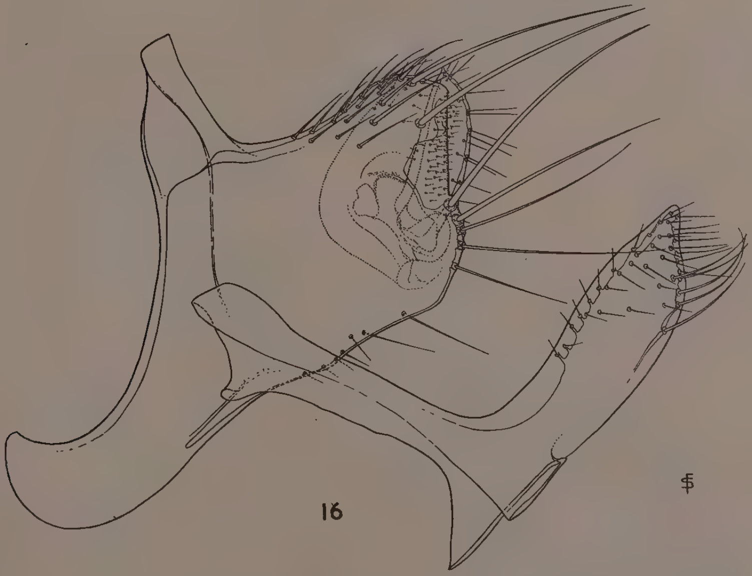

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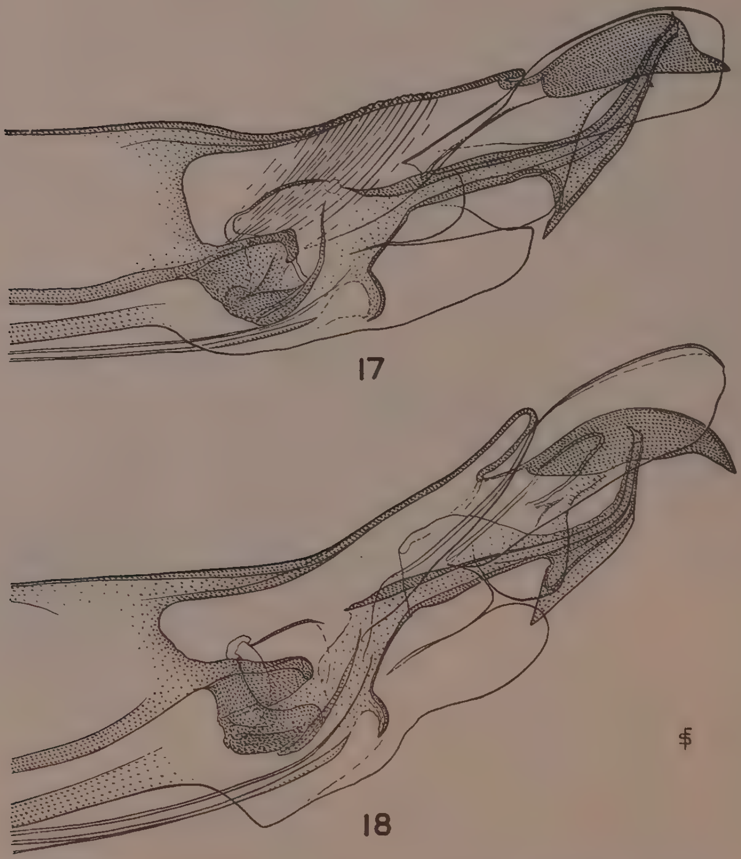
FIGS. 15–16.—Clasper and sternum IX of: (15) *Tetrapsyllus amplus* (Jordan and Rothschild) (holotype); (16) *Tetrapsyllus rhombus* sp. n. (holotype).

Tetrapsyllus rhombus sp. n. (Figs. 16, 18, 19, 21.)

Male holotype *ex Oryzomys longicaudatus*, 8.vii.1952; female allotype *ex Euneomys dabbenei*, 8.vii.1952. Paratypes: *ex Akodon neocenus*: 1 ♀, 8.vii.1953; *ex Abrothrix hirta modestior*: 1 ♀, 5.vii.1952; *ex Oryzomys longicaudatus*: 3 ♂, 8 and 14.vii.1952; 1 ♂ 1 ♀, 25 and 26.ii.1954; from nest of *Notiomys valdivianus fossor*: 2 ♂, 27.ii.1954; ex *Rattus* sp.: 1 ♂, 6.vii.1952; from nest of *Rattus norvegicus*: 1 ♂ 4 ♀, 20.ii.1954.

Closely related to *Tetrapsyllus amplus* (Jordan and Rothschild), 1923, from which it differs in the male by the structure of the genitalia: the new species has an apically broader corpus of clasper, a narrower distal arm of the ninth sternum and the phallosome, although of the same pattern, is different in a number of details. Females can be distinguished from those of *T. amplus* by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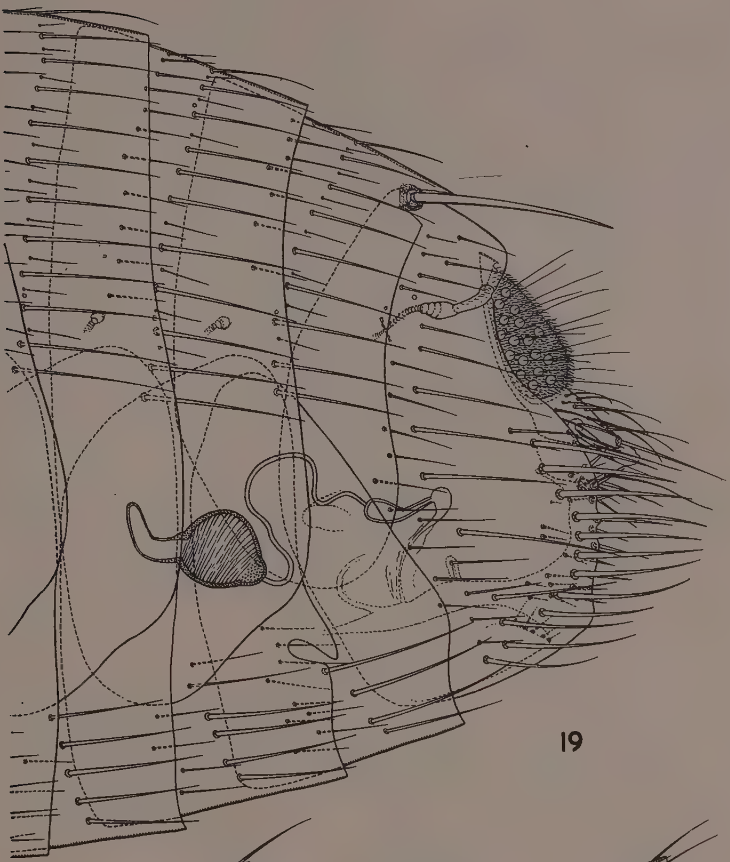
Figs. 17–18.—Aedeagus of: (17) *Tetrapsyllus amplus* (Jordan and Rothschild) (holotype); (18) *Tetrapsyllus rhombus* sp. n. (holotype).



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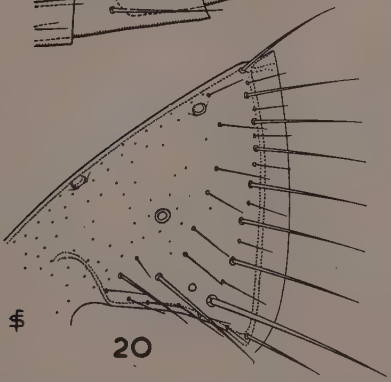

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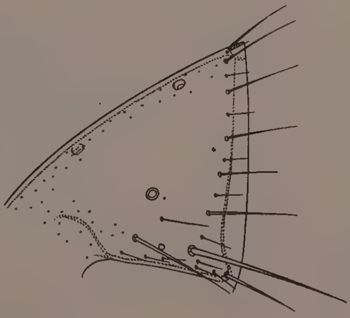

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Figs. 19, 21.—*Tetrapsyllus rhombus* sp. n. (19) Terminal segments of female (allotype). (21) Postantennal region of head of female (allotype).

Fig. 20.—*Tetrapsyllus amplus* (Jordan and Rothschild). Postantennal region of head of female (paratype).

the absence (or reduction to one seta) of the penultimate occipital row of setae; the posterior margin of sternum VII is less markedly bent.

Except for the difference in the chaetotaxy of the head of the female mentioned above (fig. 21, cf. fig. 20), the non-genitalic structures are much the same as those of *T. amplus*, so that a description of these is unnecessary.

Modified abdominal segments, male (figs. 16 and 18).—Manubrium of clasper broader than that of *T. amplus* (fig. 16, cf. fig. 15). Corpus of clasper rhomboid, its dorso-posterior part being more strongly developed than in *T. amplus*, consequently the posterior margin is longer in the new species. Movable process of clasper straight, tapering to a pointed apex, its anterior margin without a blunt angle near the middle; on its inner surface with many small setae as in *T. amplus*. The apex of the movable process extends only a little above the dorsal margin of the corpus of clasper, whereas in *T. amplus* it extends for a much greater part. Chaetotaxy of clasper, as well as of sternum IX, similar to that of *T. amplus*. The heel of sternum IX is longer than in *T. amplus* and so is the sclerotisation of the ventral margin adjoining the heel. Distal arm of sternum IX a little expanded in its apical half, basally narrower and apically much more pointed than that of *T. amplus*. Differences in the phallosome between the two species are fairly considerable and the most striking are: dorsal margin of crochet evenly convex in *T. rhombus* instead of being apically inflated as in *T. amplus*; the fold in the dorsal margin is much greater and anterior to this the lateral surface of the aedeagus is not striated, as it is in *T. amplus*; the inner tube of the aedeagus is apically straighter, and its ventral triangular expansion has the sclerotic ridge situated well away from the ventral margin (fig. 18, contrast fig. 17).

Female (fig. 19).—Sternum VI with a narrow and fairly deep sinus, more or less similar to that of *T. amplus*. Posterior margin of sternum VII with a slight bulge, below which the margin is concave. Spermatheca and genital ducts very much like those of *T. amplus*.

Remarks.—As part of the description of *Tetrapsyllus amplus* (1933, *Ectoparasites* 1: 366), Jordan and Rothschild "also figure the tail-end of a ♀ from Lake Epuyen, Chubut, which is slightly different and possibly represents an Argentinian race (text-fig. 381)". Comparison of this female and the ones recorded in the original description as *T.* "*amplus*" from Temuco, Chile, and Cholila, Chubut, with females of *T. rhombus* revealed that these

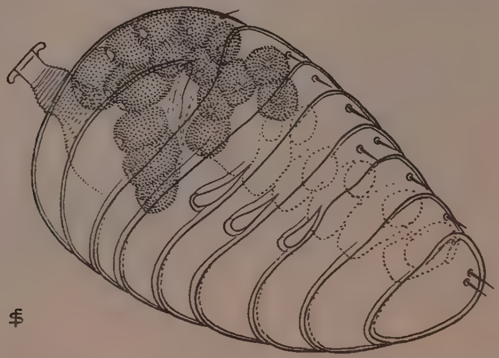

FIG. 22.—Antennal clava of *Tetrapsyllus tantillus* (Jordan and Rothschild) (female, from Bariloche; in this specimen the second segment of the clava is reduced, which is abnormal).

three female paratypes belong to *T. rhombus* and not to *T. amplus*, which is now only known from Valparaiso, Chile (type locality).

Note on the antenna of species of Tetrapsyllus.

Whilst studying specimens of *Tetrapsyllus* it struck me that the antennal clava in every specimen of all species examined contains what I at first called " a bunch of grapes ". Inside the basal half of the clava are a number of globular objects, each of which has one small circular hole. The majority of these globules lie close against each other, and their sides are flattened where they touch (fig. 22). All the globules inside one clava are grouped together and they no doubt have the same function (whatever that may be) ; thus they constitute one organ, which I propose to call the *uvoid organ*. I have not seen this most peculiar organ in any other fleas and the presence of it is therefore an important characteristic of the genus *Tetrapsyllus*.

Ectinorus onychius onychius (Jordan and Rothschild), 1923. (Figs. 23, 24.)

Ex Euneomys dabbenei : 1 ♀, 8.vii.1953 ; *ex Oryzomys longicaudatus* : 2 ♂, 26.ii.1954 ; from nest of *Notiomys valdivianus fossor* : 3 ♂ 3 ♀, 27.ii.1954 ; *ex Rattus* sp. : 1 ♂, 12.vii.1952 : from nest of *Rattus norvegicus* : 3 ♂ 1 ♀, 20.ii.1954.

This flea was only known from the male holotype and one male paratype, collected at Cholila, Chubut Territory, Argentina, *ex Ctenomys haigi* and *Akodon iniscatus*. A description of the female is given below.

A description of the terminal segments would suffice, but since no figure of

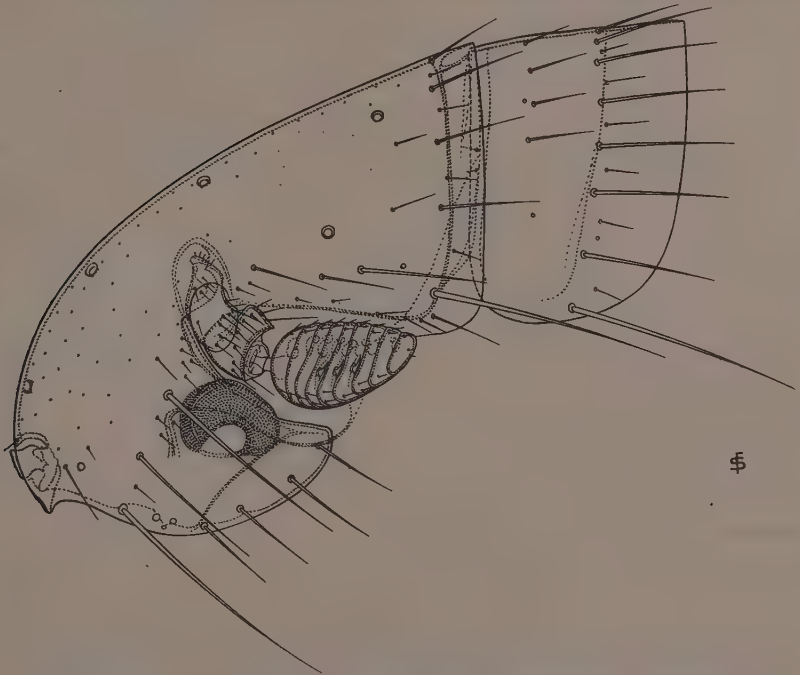

FIG. 23.—*Ectinorus onychius onychius* (Jordan and Rothschild). Head and pronotum of female (from Bariloche).

the head of any member of the genus *Ectinorus* has ever been published, I have prepared one of the head and pronotum of a female of *E. o. onychius* (fig. 23).

Jordan and Rothschild (1923, *Ectoparasites* **1**: 354) mention that in the male paratype of *E. o. onychius* the pronotum bears three pseudosetae on the inner surface of the collar each side; this is abnormal in the genus (as it is in nearly all genera). One of the specimens (a male) recorded above also has this

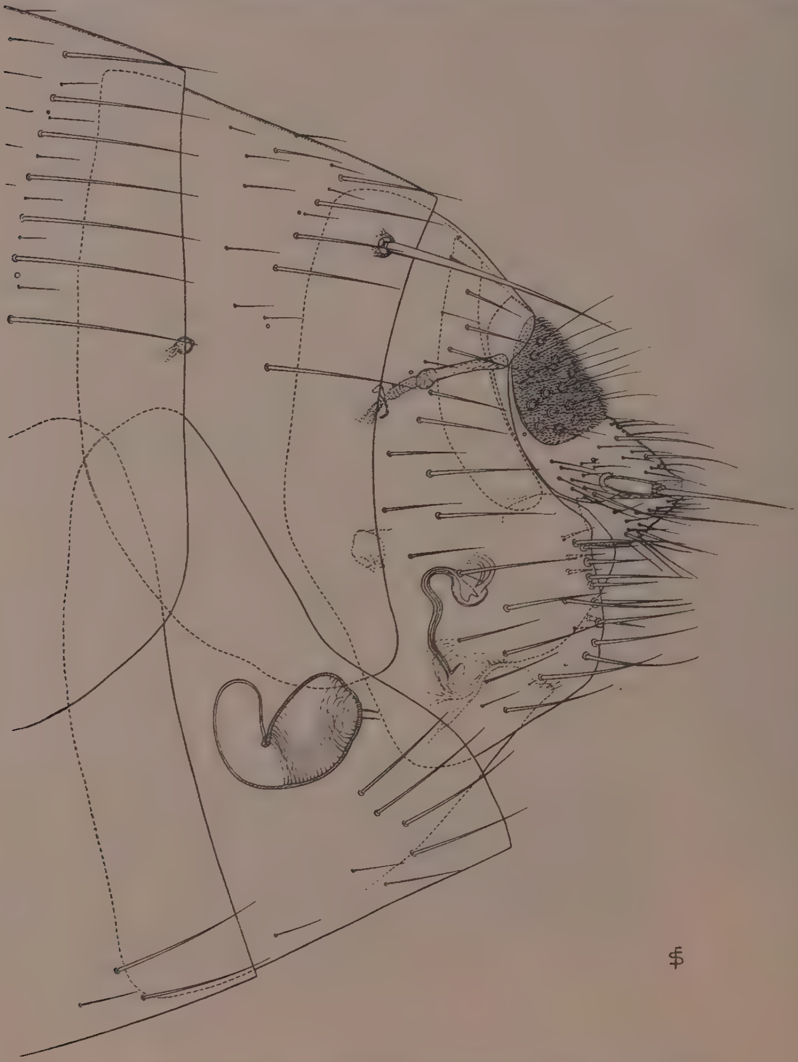

FIG. 24.—*Ectinorus onychius onychius* (Jordan and Rothschild). Terminal segments of female (from Bariloche).

peculiarity, although this specimen has only one pseudoseta on one side of the pronotal collar and none on the other.

Female. Terminal segments and genitalia (fig. 24).—Antesensilial seta on a submarginal pedestal. Posterior margin of sternum VII slightly sigmoid, without a sinus; sternum VII with a main row of about four setae. Tergum VIII with about 20 setae extending from near the dorsal margin to near the ventral margin. Sensilium with 17 trichobothria each side. Anal stylet about four times as long as broad, with one long apical seta and three short preapical setae. Ductus bursae and bursa copulatrix strongly sclerotised; a fairly long ductus obturatus is present. Bulga of spermatheca roughly rectangular, with a fairly thin wall; hilla rather broad and without inner striations.

Family CERATOPHYLLIDAE.

Nosopsyllus fasciatus (Bosc), 1800.

Nosopsyllus endymionis (Rothschild), 1904, *Novit. zool.* **11**: 634. **Syn. nov.**

Ex Oryzomys longicaudatus: 1 ♂, 12.vii.1953; *ex Rattus* sp.: 1 ♀, 12.vii. 1952; from nest of *Rattus norvegicus*: 21 ♂ 43 ♀, 20.ii.1954.

This cosmopolitan parasite of *Rattus* belongs to an old-world genus and has been dispersed all over the world by means of ship-rats. *N. fasciatus* was already known from South America, where it had been found in Chile (Santiago and Valparaiso); Argentina (Buenos Aires and Santa Fe) and Brazil (State of São Paulo). Chilean specimens were described by Rothschild (1904, *Novit. zool.* **11**: 634) as *Ceratophyllus endymionis* (referred to *Nosopsyllus* by Jordan, 1933, *Novit. zool.* **39**: 77). I have examined the type-material and it is beyond doubt that the name *Nosopsyllus endymionis* (Rothschild), 1904, is a synonym of *N. fasciatus* (Bosc), 1800, the specimens being merely individual variations.

An interesting fact, emerging from the study of the fleas recorded above, is that the flea-fauna from Temuco, Chile, southwards through the Bariloche district to the Chubut Territory (inclusive) is uniform, most of the fleas known from there not occurring to the north of this part of Patagonia. The apparent absence of species of the large genus *Polygenis* in the Temuco-Chubut area is striking. In addition to the fleas recorded above, the following fleas (not yet collected at Bariloche) are known to occur in the Temuco-Chubut area: Temuco, Prov. of Cautín, Chile: the bird-fleas *Dasypsyllus araucanus* (Jordan and Rothschild) (*ex Taenioptera pyrope*) and *D. cteniopus* (Jordan and Rothschild) (*ex Scytalopus magellanicus*); Chubut Territory, Argentina: Cholila: *Ectinorus levipes* (Jordan and Rothschild) (*ex Ctenomys haigi*) and *Listronius fortis* (Jordan and Rothschild) (*ex Akodon iniscatus*); Leleque: *Listronius ulus* (Jordan and Rothschild) (*ex Abrothrix suffusus*); Techa: *Tiamastus subtilis* (Jordan and Rothschild) (*ex Phylotis xanthopygus*).

" To find out this connection, the blood-relationship, is the ultimate aim of the classifier. The descriptive part of classificatory work provides the necessary facts; the classification is a summary of the conclusions the classifier bases upon these facts. The correctness of the classification, therefore, depends firstly on the trustworthiness and the degree of completeness of the observations, and, if this evidence can be relied upon, secondly on the interpretation of the facts.

" Now, in weighing off the evidence systematists follow two very different methods. The first method, a relic from pre-Darwinian times, is by far the dominant one in ordinary systematic work, because it is so very convenient; it consists in taking as the basis of the primary division of the group (and subsequently of each subgroup and minor division) certain distinguishing characters which the respective classifier assumes to be of primary importance, without giving any reason (1) why the forms which possess that character are closer related to each other than to forms which do not possess it, and (2)—and this is the point where the grave mistake comes in—why the forms that are devoid of that character are all phylogenetically closer connected with each other than with forms which have the respective character. It is obvious that the result of this method entirely depends on what characters the classifier selects for gradually dividing up the group of forms, and, as the selection is arbitrary inasmuch as the phyletic significance of the selected character is merely assumed to be warranted, that the classification is based on a string of assumptions. Hence it is self-evident that the classifications drawn up by different authors according to this method must naturally deviate widely from one another, if the classifiers do not make the same assumptions; and as there is no reason why they should select the same distinguishing characters and use them in the same order, the antagonistic results of different authors are merely antagonistic assumptions."

(Jordan, K., 1898, *Novit. zool.* **5** : 397–398)

TWO NEW SUBSPECIES OF FLEAS (SIPHONAPTERA) FROM THE BRITISH ISLES

By F. G. A. M. Smit

WITH A DISCUSSION ON THEIR DISTRIBUTION

By Miriam Rothschild and F. G. A. M. Smit.

With 86 Text-figures.

> "*Study the variation of a single common species and spend your holidays in the districts where its subspecies meet.*" (Jordan, 1940, *Int. Congr. Ent. VI* (Madrid) : 151.)

During the past twenty years Dr. Jordan has made a special study of subspeciation in fleas and has paid particular attention to the flea of European Field Mice and Voles, *Ctenophthalmus agyrtes*. It is a great honour to be asked to contribute to his jubilee volume, and I have tried to select a subject which will be of some special interest to him. In the following pages I have therefore touched upon some problems arising from a study of the variation in Britain of two common fleas: *Ctenophthalmus nobilis* (Rothschild), which is the British representative of the *agyrtes* complex, and the Sand Martin flea *Ceratophyllus styx* Rothschild.

Acknowledgments.

I am greatly indebted to the Hon. Miriam Rothschild for suggesting (in 1948) the study of *Ceratophyllus styx* and *Ctenophthalmus nobilis* in Britain, reading my manuscript and collaborating with me in the theoretical discussion. The following colleagues kindly provided us with specimens for comparison and for the collection : Mr. R. M. Allan, Mr. F. A. Bak, Mr. J. K. Bates, Mr. R. S. George, Mr. R. A. O. Hickling, Dr. W. D. Hincks, Mr. C. Matheson, Mr. E. C. Newman, Dr. I. D. Pennie, Mr. G. B. Thompson, Professor G. C. Varley, Mr. George Waterston and Mr. Kenneth Williamson. We are also most grateful to Dr. B. P. Beirne, Dr. E. A. Cockayne, Dr. E. B. Ford, Dr. R. E. Moreau and Professor O. W. Richards for many helpful suggestions regarding the distribution of the hosts and various Lepidoptera and Hymenoptera. Mr. G. H. E. Hopkins has kindly read and criticised the manuscript for us both.

Ctenophthalmus nobilis (Rothschild).

It is usual practice to accord *Ctenophthalmus nobilis*[1] subspecific status only,

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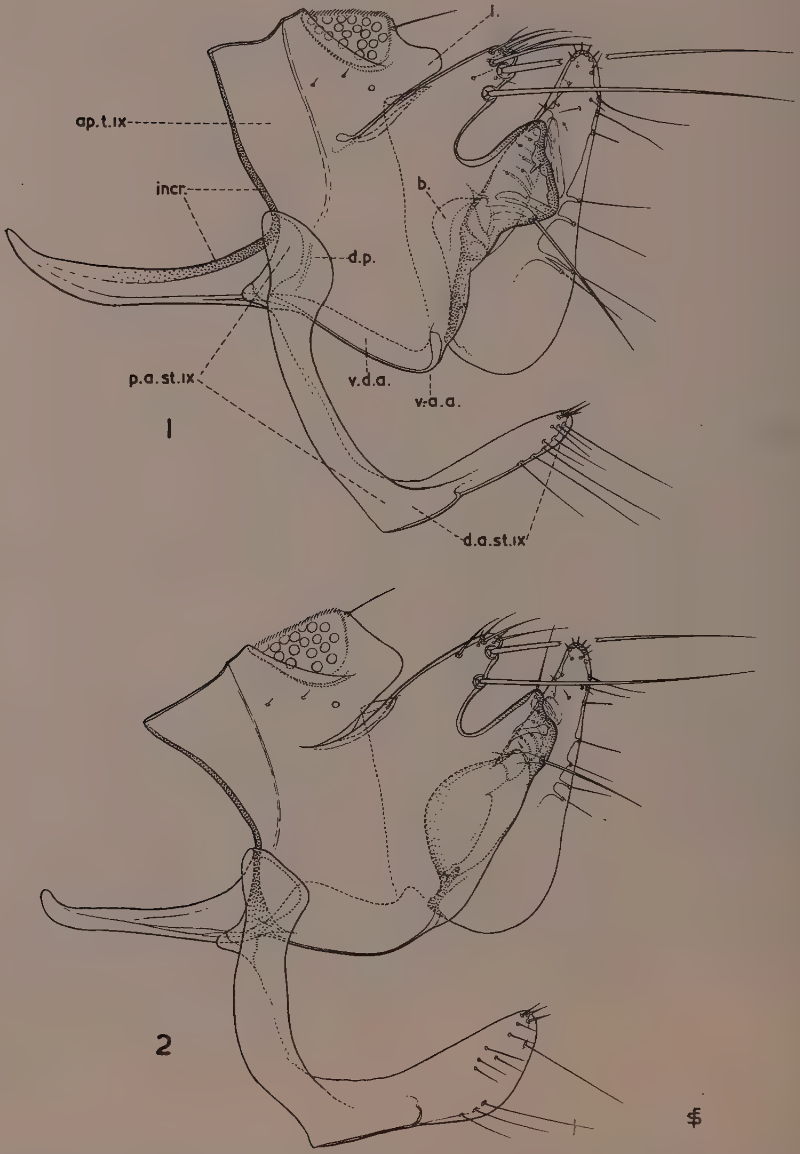
[1] Rothschild (1898 : 538, pl. 15A, figs. 1, 2, pl. 17, figs. 12, 14, 17–25) was the first to identify British specimens of the mouse flea in question as *Typhlopsylla agyrtes* Heller, 1896 (= *Ctenophthalmus agyrtes* (Heller)) ; earlier British authors had misidentified the species as *Typhlopsylla assimilis* Taschenberg, 1880. In 1922 Jordan and Rothschild described (p. 282) a subspecific distinction between the British and Continental *agyrtes* and named the British form *Ctenophthalmus agyrtes celticus* ; but according to the Rules of Zoological Nomenclature the correct name for this taxon is *nobilis*, first used by Rothschild in 1898 : 539.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1
d.a.st.ix
2

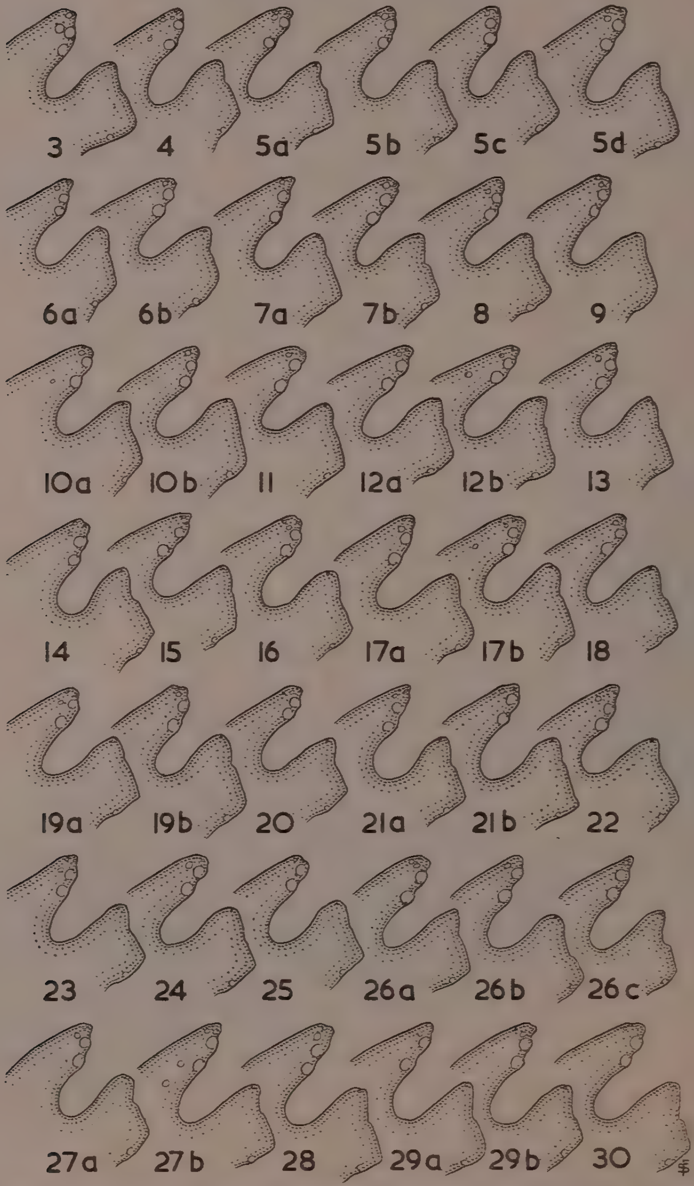
Figs. 1–2.—(1) *Ctenophthalmus nobilis nobilis* (Rothschild). Clasper and sternum IX (Stonegate, Sussex). (2) *Ctenophthalmus agyrtes impavidus* Jordan. Clasper and sternum IX (Merano, Dolomites).

and I must therefore give my reasons for raising it to the rank of a full species. Since 1922, when *celticus* was described as a subspecies of *Ctenophthalmus agyrtes*, Jordan and Wagner have both expressed the view that it might perhaps be a full species. Jordan (1938 : 109) remarked on the structure of the ventral lateral lobe of the aedeagus and said : " *nobilis* differs therein from all other subspecies of *Ct. agyrtes*, and from the purely morphological point of view therefore has some claim to specific distinctness". Wagner (1939 : 236–237) also dealt with this aedeagal lobe and stated : " Was die taxonomische Bedeutung dieses Merkmals betrifft, so bin ich nicht nur mit der Meinung Jordan's ganz einverstanden, sondern nehme ich auch als sehr wahrscheinlich an, dass der britische *Ctenophthalmus* überhaupt keine Subspecies, sondern eine selbständige Art darstellt, welche sich im männlichen Geschlecht durch die Form und die Beborstung des 9. Sternits und im weiblichen meistenteils durch den Apikalrand des 7. Sternits recht gut unterscheiden lässt."

The criteria for determining a form as a species or a subspecies are : (*a*) the degree of morphological differences, (*b*) the geographical relationships, and (*c*) whether or not different forms are reproductively isolated. Each of these three factors will be examined here in relation to *nobilis*.

(a) *The degree of morphological differences.*—As already noted by Jordan, *nobilis* differs from all subspecies of *C. agyrtes* in the structure of the ventro-lateral aedeagal lobe ; Wagner added to this the shape and chaetotaxy of sternum IX in the male and the shape of the posterior margin of sternum VII in the female. There are several other distinctions, and a list of all the differences I have found between *C. nobilis* and the polytypic species *C. agyrtes* is given below.

Male (fig. 1, contrast fig. 2) : (1) The posterior margin of sternum VIII is smoothly rounded ; in *agyrtes* it is more or less distinctly angulate dorsally and ventrally. (2) The apodeme of tergum IX (*ap. t.* IX) is more or less rectangular ; in *agyrtes* roughly triangular. (3) The angle formed by the anterior margin of the tergal apodeme and the dorsal margin of the manubrium is about 90° ; in *agyrtes* usually much less. (4) The incrassation of the anterior margin of the tergal apodeme (*incr.*) continues without a break along the dorsal margin of the manubrium ; in *agyrtes* the incrassation continues in a downward direction instead of following the dorsal margin of the manubrium. Probably this structural modification is correlated with the degree of reduction of the ninth sternum, in which the dorsal end of the proximal arm is connected to the apex of the manubrium by muscles. (5) The ventro-apical angle of the body of the clasper (*v.-a. a.*) is about 90° ; in *agyrtes* wider and therefore less marked. (6) The posterior margin of the tergum behind the sensilium is drawn out into a rounded lobe (*l.*) ; in most *agyrtes* subspecies this lobe is poorly developed or absent. (7) The acetabular portion of the movable process has a much reduced " bulge " (*b.*) ; in *agyrtes* this bulge is always large. (8) The ventral demarcated area of the body of the clasper (*v.d.a.*) is much narrower than in *agyrtes*. (9) The widened dorsal part (*d.p.*) of the proximal arm of sternum IX is smoothly rounded posteriorly ; in *agyrtes* it is distinctly angulate. (10) The proximal arm of sternum IX (*p.a.st.* IX) is rather narrow and fairly straight ; in *agyrtes* it is broader and more strongly curved. (11) The distal arm of sternum IX (*d.a.st.* IX) is very narrow and resembles that of *C. apertus* sspp. ; in *agyrtes* this arm is much broader. (12) The ventro-lateral lobe of the aedeagus is turned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FIGS. 3–30—*Ctenophthalmus nobilis nobilis* (Rothschild); fixed processes of clasper of specimens from: (3) Moulsecombe (topotype); (4) Iden nr. Rye; (5) Stonegate; (6) Lyndhurst; (7) Horton Kirby; (8) Isle of Sheppey; (9) Hockley; (10) Osea Island; (11) nr. Ipswich; (12) Elveden; (13) Eriswell; (14) Blakeney Point; (15) King's Lynn; (16) Elsworth; (17) Boxworth; (18) Woburn; (19) Ashton, Oundle; (20) Spurn; (21) Tring; (22) Hilton; (23) South Ronaldshay; (24) Craigiebuckler; (25) Whiteparish; (26) Isle of Wight; (27) North Bull Island; (28) St. Annes; (29) Rockey Valley; (30) Bundoran.

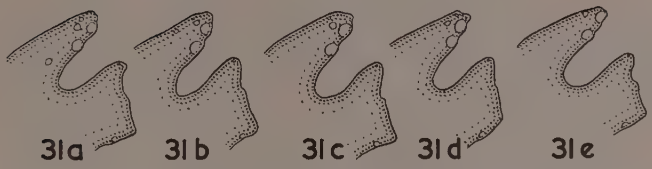
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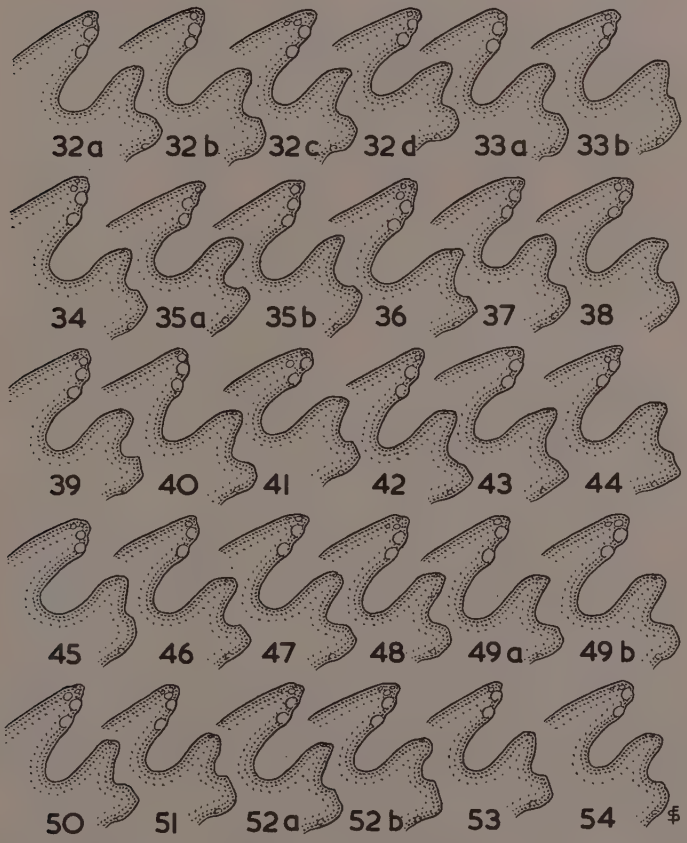
Fig. 31.—*Ctenophthalmus nobilis nobilis* (Rothschild); fixed processes of clasper of specimens from Royat-les-Bains, France.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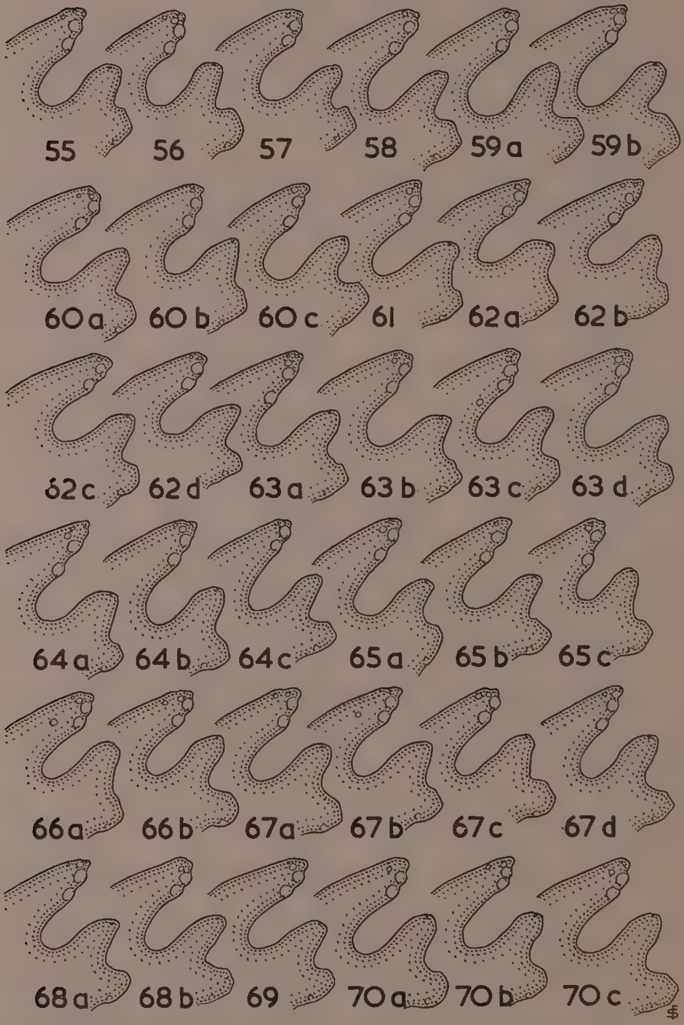
Figs. 32–54.—*Ctenophthalmus nobilis vulgaris* Smit; fixed processes of clasper of specimens from: (32) Stornoway; (33) Pabbay; (34) Islay; (35) Lunga; (36) Hoy; (37) Sanday; (38) Fair Isle; (39) Mull; (40) Ackergill; (41) Achmore; (42) Glenfinart; (43) Benmore; (44) Kinloch Rannoch; (45) Struan; (46) Newcastleton; (47) Balminnoch; (48) Oakbank; (49) North Berwick; (50) Rhossili; (51) Gloucester; (52) Brookethorpe; (53) Wilstone nr. Tring; (54) Braunton.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70 a
70 b
70 c

FIGS. 55–70.—*Ctenophthalmus nobilis vulgaris* Smit; fixed processes of clasper of specimens from: (55) Braunton; (56) Hartland Quay; (57) St. Ives; (58) Rilla Mill (holotype); (59) Tresco; (60) Belmullet; (61) Bundoran; (62) St. Martin, Jersey; (63) St. Jacut; (64) 2½ km. west of Bagnoles de l'Orne; (65) "outside" Bagnoles de l'Orne; (66) Poitiers; (67) Ruffec; (68) Condac; (69) Villefagnan; (70) Lignières.

upward, has a serrated margin and is only partly clad with "scales"; in *agyrtes* this lobe may also be turned upward, but its margin is not serrated although it may appear to be so because of overhanging "scales", which here cover the whole of an upturned lobe. *Female*: (13) The posterior margin of sternum VII possesses a well-developed, long and narrow lobe below the large dorsal lobe; in *agyrtes* this lobe is much reduced and sometimes hardly discernible. Although the differences between *agyrtes* and *nobilis* in each character are not great, it is the sum of these differences that contrasts *nobilis* with *agyrtes* s.l., so that on a morphological basis *nobilis* can certainly claim specific distinctness.

(b) *Geographical relationships.*—In the British Isles *C. nobilis* is, of course, completely isolated geographically from the continental subspecies of *agyrtes*. In France it appears to be geographically isolated (an apparent exception is discussed below), but further collecting, particularly in northern and western France, is necessary before this can be finally decided.

(c) *Reproductive isolation.*—There is ample evidence that the subspecies of *agyrtes* are not isolated reproductively, and the zone of transition where two subspecies interbreed is usually fairly broad—several miles at least. For example, Peus (1950 : 302) mentions that near Lengerich, Westphalia, the zone of transition between *C. a. agyrtes* and *C. a. smitianus* has a width of about six kilometres (just under four miles) ; I found similar and wider zones of transition between these two subspecies in Holland. Intermediate males have been found between several other pairs of subspecies of *agyrtes*. As a rule reproductive isolation is most difficult to determine in the field, but in the case dealt with here we are extremely fortunate that Dr. Jordan (in 1932) discovered a locality in France (Bagnoles de l'Orne, Normandy) where *nobilis* met *agyrtes impavidus* (not *agyrtes agyrtes*, as stated in Jordan 1938 and 1940), and where he discerned no sign of interbreeding though the two different forms were found to live only a few hundred yards apart.[2] Furthermore, they appeared to be restricted to definite and different biotopes. Jordan (1940 : 151) remarked : " . . . as no intermediate specimens were found, one would further conclude that interbreeding did not take place, which would prove the two races really to have the status of distinct species. . . . The two races are not in contact with each other at Bagnoles ; I cannot guess the reason why one keeps there to the woods and the other to the hedgerows and fields outside, and it is quite likely that in other places in Normandy the races behave differently. If the restriction to biotopes as at Bagnoles is the rule for this mouse-flea in Normandy, the ranges of the two races do not overlap, but fit into one another like the tongues of match boarding. I should have been much more pleased if I had found the races occurring on the same specimens of the host and interbreeding ; it would have settled at least that point."

It is disputable whether the two forms were in contact at Bagnoles or not, for : " The intermediate ground was occupied by houses and gardens where I could not put up any traps " (Jordan 1938 : 105). But one might expect mice to traverse this area and they would certainly intermingle at either end of this small built-up plot ; also, mice must have had a free run of the area before any building began. *C. nobilis* and *a. impavidus* were each found on *Apodemus sylvaticus* and *Clethrionomys glareolus* in their respective biotopes at Bagnoles. In any case, a zone of hybridisation would be much wider than a few hundred yards. Jordan's careful observations therefore suggest very strongly that interbreeding does not take place and the two forms are separate species.

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[2] M. Rothschild recently (Aug.–Sept., 1955) collected in the same garden at Reux, nr. Pont l'Evêque, (Calvados), France : 1 ♂ *C. agyrtes impavidus* (from *Sorex minutus*) and 1 ♂ *C. nobilis vulgaris* (from *Apodemus sylvaticus*). This discovery proves that both species of fleas are in contact with each other (at least at Reux). Further collecting in north-western France is desirable ; I myself collected at Maromme and Pavilly (Seine inférieure), but obtained there only a number of *C. agyrtes impavidus*.

Items (a) and (c), taken together, provide strong evidence that *nobilis* should be accorded specific rank. There is, however, not the slightest doubt that *nobilis* is very closely related to *agyrtes*, in fact probably once was a subspecies of *agyrtes*, and it is therefore unfortunate that by giving *nobilis* specific status this close relationship becomes obscured.

C. nobilis plus *C. agyrtes* s.l. probably form a superspecies (Artenkreis of Rensch), and it is regrettable that no satisfactory method has been found to distinguish this category by a special nomenclature. Mayr *et al.* (1953 : 29) define a superspecies as "a monophyletic group of very closely related and largely or entirely allopatric species." I understand that the term "species" in this concept may mean both monotypic and polytypic species.

Variation in Ctenophthalmus nobilis.—Jordan (1931 : figs. 6, 6*a*) figured part of the clasper of two specimens to illustrate the variability of "process P" of *nobilis* and mentioned (1931 : 138) the individual variation of this flea, but did not deal further with this subject. Peus (1950 : 229) came to more positive conclusions and states: " . . . zeigt der P^2 [Jordan's "process P"] dort [i.e., British Isles] eine deutliche Variation, die über die vorhandene individuelle Variabilität hinaus insofern geographisch scheint geordnet werden zu können (?), als der Ausschnitt des P^2 im Norden tiefer ist, wodurch der dorsale Zapfen des P^2 stärker hervorragt; es bleibt aber zu prüfen, ob es sich dabei um subtile Rassenverschiedenheit handelt, für die, wenn sie gegeben sein sollte, die Grenze vielleicht etwa in der Höhe von Oxford zu suchen wäre. Allen britischen Tieren ist die mehr oder weniger geradlinige Abstutzung des unteren Zapfens des P^2 gemeinsam. In Westfrankreich geht diese Abstutzung verloren, der genannte Zapfen wird ± rund; ein mir verfügbares ♂ von Poitiers (Abb. 8 F) zeichnet sich durch besonders tiefen Ausschnitt des P^2 aus (individuell ?), während an der Nordküste (Abb. 8 E) noch nähere Beziehungen zu England zu bestehen scheinen. Bei einem ♂ aus Südfrankreich [Royat-les-Bains, Puy de Dôme district] schliesslich, nahe der Grenze zu *apertus*, zeigt der P^2 gar keinen Ausschnitt (Abb. 8 G) und ist der F sehr schmal, so dass hier vielleicht eine besondere Subtilrasse vorliegt."

In December, 1953, my brother-in-law, Jhr. J. van Heurn, kindly collected some field-mouse fleas for me in Sussex, mainly specimens of *nobilis*, and it struck me that in all these males P^2 lacked a sinus. Since Peus came to his interesting conclusions on the basis of a study of only a relatively small number of specimens, I felt it advisable to check the variability of P^2 in all the specimens available in the Tring collection (about 1700 specimens). The study of this material showed that certain populations are characterised by a non-sinuate P^2, while members of most populations have a distinct sinus in this process. These two forms are regarded as distinct subspecies, and that with a sinus in P^2 is described below. The holotype of *C. nobilis* is a female, collected by the Brazenor brothers at Brighton, Sussex, from *Arvicola terrestris*, on 31st May, 1897. It is unfortunate that this holotype is a female, for the two subspecies of *C. nobilis* are indistinguishable in this sex, but there is in the Tring collection one male topotype (from Moulsecombe, roughly two miles N.E. of the base of Brighton's West Pier, from *Talpa europaea*, May, 1901, also collected by the Brazenor brothers) and this is a typical specimen of the form with no sinus in P^2, which

I therefore regard as the nominate subspecies—for all practical purposes this topotype functions as a holotype. It should be noted that specimens from not far west of Brighton (Worthing, Goring-on-Sea) are intermediate between the two subspecies. The situation would have been extremely awkward if the holotype of *C. nobilis* had been intermediate between the two subspecies, and this raises *a nomenclatorial question of considerable interest*: if this topotype had been perfectly intermediate between the two subspecies, or if the holotype of *nobilis* had been an intermediate male, to which of the two subspecies should the name *C. nobilis nobilis* have been restricted ? So far as I am aware the International Rules of Zoological Nomenclature make no provision for such cases, yet if the type-locality of *nobilis* had been as little as ten miles further west we should almost certainly have been faced with the problem in this instance. The only satisfactory solution in such a case would be to set aside the holotype and make a neotype which was definitely of one or the other subspecies, but this would be entirely contrary to the present rules of nomenclature.

Ctenophthalmus nobilis **vulgaris** subsp. n.

Type material: Male holotype (fig. 58), CORNWALL: Rilla Mill, *ex Arvicola terrestris*, 3.vi.1905 (*K. Jordan*); three male paratypes, same locality and date, but *ex Clethrionomys glareolus*.

This subspecies differs from *C. n. nobilis* (Rothschild), 1898, by the process P^2 of the clasper being sinuate, the width of its lower lobe being less than half the width of the process (figs. 32–70). In the nominate subspecies a sinus is at most indicated, and the width of the lower lobe is usually greater than half that of P^2 (fig. 1, 3–31). Females of the two subspecies are inseparable.

Distribution of the two subspecies, based on material examined (see maps, figs. 80, 81 on p. 358, 359 of this volume):

C. n. nobilis (Rothschild); BRITISH ISLES: *England*[3]: Bedfordshire (Woburn (fig. 18)); Berkshire (Bagley Wood, Calcott, Tilehurst); Cambridgeshire (Boxworth (fig. 17*a*, *b*), Cambridge, Cherry Hinton, Elsworth (fig. 16)); Essex (Hockley (fig. 9), Rayleigh); Hampshire (Lyndhurst (fig. 6*a*, *b*)); Hertfordshire (Felden, St. Albans, Tring (fig. 21*a*, *b*)); Kent (Cliftonville, Horton Kirby (fig. 7*a*, *b*)); Norfolk (Blakeney Point (fig. 14), Foulsham, King's Lynn (fig. 15)); Northamptonshire (Ashton (fig. 19*a*, *b*), Northampton, Oundle); Osea Island (fig. 10); Oxfordshire (Oxford); Sheppey (island) (fig. 8); Suffolk (Elveden (fig. 12*a*, *b*), Eriswell (fig. 13), Ipswich (fig. 11), Newmarket); Surrey (Reigate, Woking); Sussex (Iden (fig. 4), Moulsecombe, nr. Brighton (fig. 3), Rye, Stonegate (fig. 1, 5*a*–*d*)); Isle of Wight (fig. 26*a*–*c*); Wiltshire (Whiteparish (fig. 25)); Yorkshire (Spurn (fig. 20)). *Wales*: Pembrokeshire (St. Davids). *Scotland*: Aberdeenshire (Craigiebuckler (fig. 24), Cults, Hilton (fig. 22), Rosehill); Orkneys (South Ronaldshay isl. (fig. 23)). *Ireland*: Donegal (Bundoran (fig. 30)); Dublin (St. Annes (fig. 28), Clontarf); North Bull. isl. (fig. 27*a*, *b*); Wicklow (Rocky Valley (fig. 29*a*, *b*)). FRANCE: Puy-de-Dôme (Royat-les-Bains (fig. 31*a*–*e*)).

C. n. vulgaris Smit: BRITISH ISLES: *England*: Cornwall (Rilla Mill (fig. 58), St. Ives (fig. 57)); Devonshire (Braunton (fig. 54, 55); Exeter (Hartland

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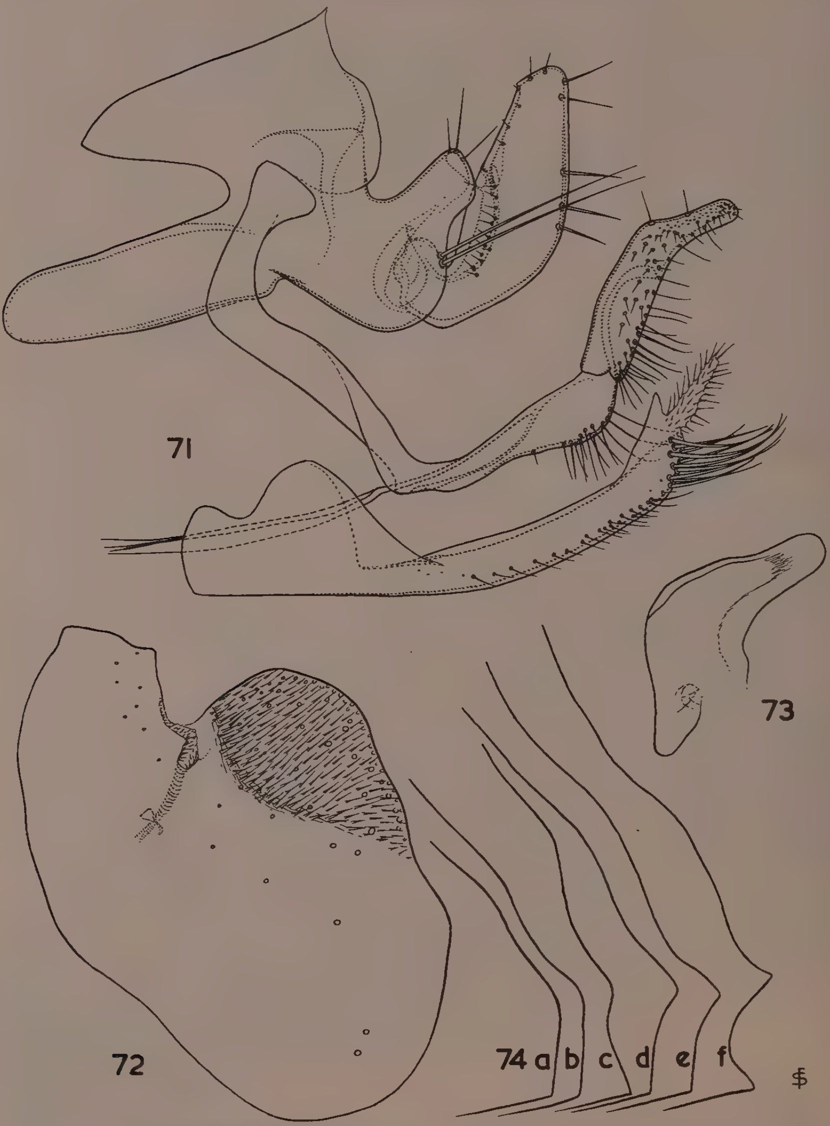
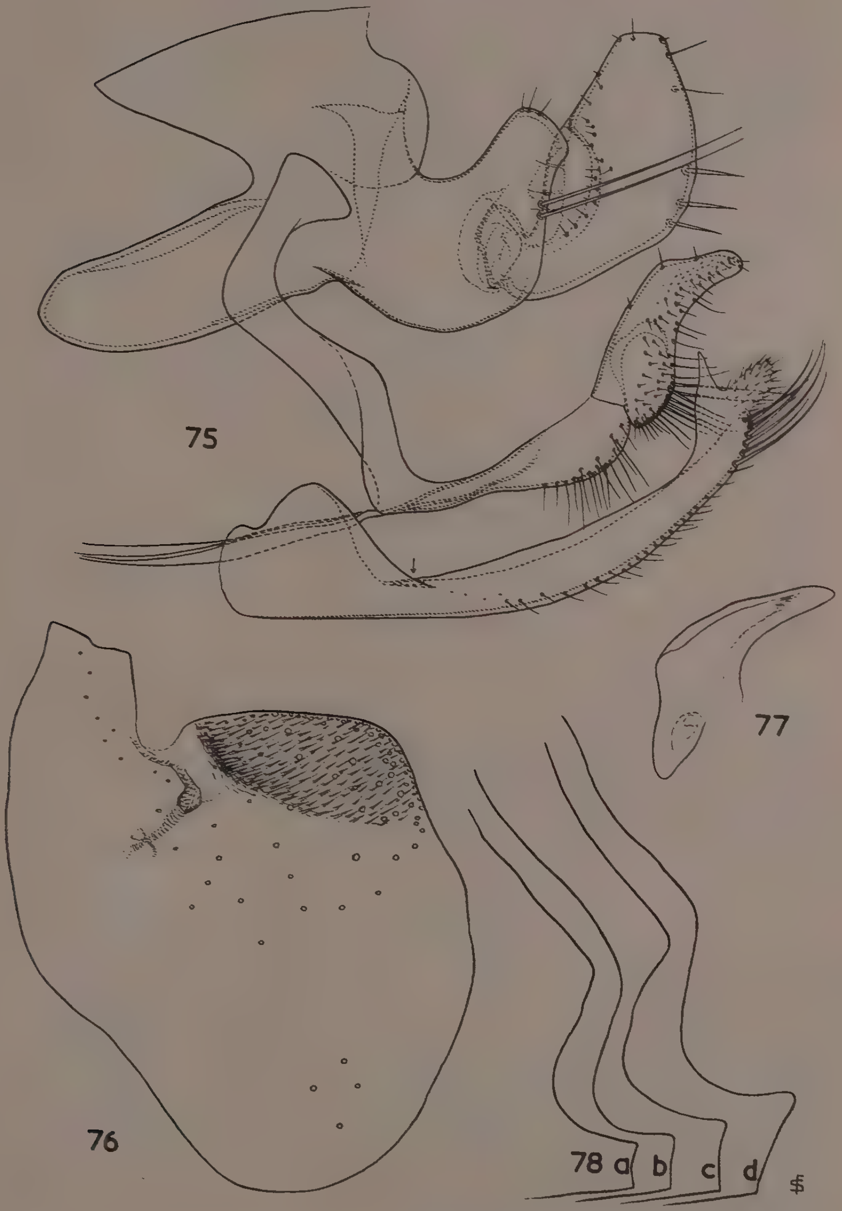
[3] The counties and localities are in alphabetical order.



Figs. 71–74.—*Ceratophyllus styx styx* Roths. (71) Clasper, sterna VIII and IX; (72) tergum VIII of male (setae omitted); (73) crochet of aedeagus; (74) outline of sternum VII of six females, to show variation. (71–73 From nr. Hamburg, Germany; 74 from Bakhuizen, Holland).

Quay (fig. 56), Salcombe); Gloucestershire (Brookethorpe (fig. 52*a*, *b*), Gloucester (fig. 51), Maisemore, Quedgeley, Tibberton, Wotton-under-Edge); Hertfordshire (St. Albans, Tring (fig. 53)); Middlesex (Northwood); Oxford-



Figs. 75–78.—*Ceratophyllus styx jordani* Smit. (75) Clasper, sterna VIII and IX; (76) tergum VIII of male (setae omitted); (77) crochet of aedeagus; (78) outline of sternum VII of four females, to show variation. (75–77 From the holotype; 78 from Tring.)

shire (Oxford); Scilly Isles (Tresco isl. (fig. 59*a*, *b*)); Sussex (Goring-on-Sea); Westmorland (Windermere). *Wales*: Cardiganshire (Aberystwyth); Glamorgan (Bishopston, Foxhole, Ilston, Oxwich, Penarth, Porteynon, Rhossili (fig. 50), Sully); Pembrokeshire (St. Davids). *Scotland*: Aberdeenshire (Oakbank (fig. 48), Scotstown); Argyllshire (Benmore (fig. 43), Glenfinart (fig. 42)); Arran isl. (Lochranza); Caithness (Ackergill (fig. 40)); Cumbrae, East Lothian (North Berwick (fig. 49*a*, *b*)); Fair Isle (fig. 38); Inverness-shire (Guisachan); Islay isl. (fig. 34); Kincardineshire (Nigg); Lewis isl. (Barvas, Stornoway (fig. 32*a*–*d*)); Lunga isl. (fig. 35*a*, *b*); Mull isl. (fig. 39); Orkneys (Hoy (fig. 36), Mainland Birsay Bay, Finstown, Stromness, Vesta Fiold), Sanday (fig. 37), Shapinshay, South Ronaldshay (Burwick); Pabbay isl. (fig. 33*a*, *b*); Perthshire (Carie nr. Rannoch, Fearnan nr. Loch Tay, Kinloch Rannoch (fig. 44), Pitlochry, Struan (fig. 45), Tyndrum); Ross and Cromarty; Roxburghshire (Newcastleton (fig. 46)); Mainland of the Shetlands (Ollaberry); Sutherland (Assynt nr. Lairg (fig. 41), Bettyhill); Wigtownshire (Balminnoch (fig. 47). *Ireland*: Donegal (Bundoran (fig. 61)); Mayo (Belmullet (fig. 60*a*–*c*)). *Channel Isles*: Guernsey, Jersey (fig. 62*a*–*d*). FRANCE[4]: Charente (Condac (fig. 68*a*, *b*), Ruffec (fig. 67*a*–*d*) and Villefagnan nr. Ruffec (fig. 69); Cher (Lignières (fig. 70*a*–*c*)); Côtes du Nord (St. Jacut-de-la-Mer (fig. 63*a*–*d*)); Orne (Bagnoles de l'Orne (fig. 64*a*–*c*, 65*a*–*c*)); Vienne (Croutelle nr. Poitiers (♀ only), Poitiers (fig. 66*a*, *b*)).

As was to be expected, a number of specimens proved to be intermediates, and they are to be found between the areas occupied by each subspecies (see fig. 80).

Intermediate specimens: BRITISH ISLES: *England*: Berkshire (Bagley Wood, Calcott, Shrivenham, Windsor Forest); Buckinghamshire (Cheddington, Drayton Beauchamp, Halton, Pitstone—all near Tring); Hertfordshire (Boxmoor, St. Albans, Tring); Middlesex (Northwood); Oxfordshire (Oxford); Somerset (Porlock Weir, Wells); Staffordshire (Dunstall); Surrey (Esher, Woking); Sussex (Goring-on-Sea, Horsham, Worthing); Isle of Wight (Newport, Ventnor); Wiltshire (Whiteparish). *Wales*: Glamorgan (Lavernock); Skomer isl. *Scotland*: Aberdeenshire (Banks of River Don, Cairney, Hilton, Kintore, Oakbank, Parkhill, Rosehill, Rubislaw); Kincardineshire (Cove, Nigg).

Ceratophyllus styx Rothschild.

A comparison of specimens of this flea from Great Britain and from the Continent has revealed constant differences of a subspecific nature between these two populations.

The only data given in Rothschild's original description of *C. styx* (1900: 543) are that it "is parasitic on the Sand Martin (Cotile riparia)" (now known as *Riparia riparia riparia*). The type series is in the N. C. Rothschild collection (British Museum (Natural History)) and was collected by G. Tate at Lyndhurst, Hampshire, on 11th July 1900, probably from a nest of the host. Only four males and one female of this series were originally mounted and one of these males is the holotype, but there were also three males and twenty-one females of the same batch in alcohol, and these have now also been mounted.

After establishing the fact (see below) that the continental Sand Martin flea is subspecifically distinct from the British form, I found to my surprise that the continental subspecies extends its range into the southern, south-eastern and eastern part of England and apparently interbreeds in places with the British subspecies, producing intermediates. Furthermore, the type series of *C. styx* Rothschild proved to consist mainly of such intermediate forms, though it includes one male of the characteristic British subspecies and a few specimens of the continental subspecies. The male holotype of *Ceratophyllus styx* Rothschild is a specimen of the continental form, which consequently becomes the nominate subspecies and must be known as *Ceratophyllus styx styx* Rothschild, 1900.

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[4] All specimens from France in the Tring collection are figured here (figs. 63–70).

The original description of *C. styx* is not very detailed and would apply to either subspecies, but figures 7 (tergum VIII of male, external side), 8 (same, internal side) and 16 (sternum VII of female) on plate ix (Rothschild, 1900) depict the continental subspecies and must have been made from specimens of the type series, for at that time there were no specimens collected on the Continent in Rothschild's collection, while the only other mounted British specimens available at the time of description came from Oundle (6 ♂, 9 ♀) and are of the British subspecies; fig. 5 on plate ix, showing the male modified segments, is most probably made from one of the intermediate specimens of the type series. In view of their early date it is not surprising that these figures are not wholly accurate; Dampf (1908 : 22, fig. 1) noticed this and published a good drawing of the modified abdominal segments of a male of the continental form, while Rothschild (1915) depicts in figs. 15 and 16, drawn by Dr. Jordan, an intermediate male and a female of the British form.[5] No drawing of a typical male of the British subspecies appears to have been published hitherto.

Since the holotype of *C. styx* belongs to the continental subspecies, the British form has no name and therefore it is named and described here and compared with the nominate subspecies, *C. s. styx*. The new subspecies occurs throughout the British Isles except in a number of localities in the south, south-east and east of England (listed at the end of the description), where it is replaced by the nominate subspecies, or alternatively intermingles with it and interbreeds with it. It should also be noted that the fact that *C. styx* has been thought to be polymorphic or dimorphic in the female (Jordan 1929 : 495, and Rothschild and Clay 1952 : 114) is due to the existence of the two subspecies which had not previously been recognised.

Ceratophyllus styx **jordani** subsp. n.

The new subspecies differs from the nominate subspecies in the following characters.

Male : The spiculose area of tergum VIII is longer than high; the proximal part of sternum VIII is relatively higher and shorter, while the distal arm is relatively longer;

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[5] Darskaya (1950 : 104) spotted the discrepancies in these drawings of British specimens of *C. styx* and says : " All the females and males that we have from Kazakhstan and the Moscow area agree well with Rothschild's first description and drawings (1900) of *C. styx* from England, and also with a drawing of a male *C. styx* from Prussia (Dampf, 1908) . . . In a later paper (1915) Rothschild gives new drawings of *C. styx* from England, drawings which differ greatly from the original figures in the width of the fixed and movable processes, and especially in the shape of sternum VII of the female. The question of the variability of *C. styx* calls for study."

the manubrium is slightly broader; the clasper and its movable process are distinctly broader; the apical lobe of sternum IX is shorter and its ventral margin basally strongly convex. *Female:* The posterior margin of sternum VII has a broad ventral lobe.

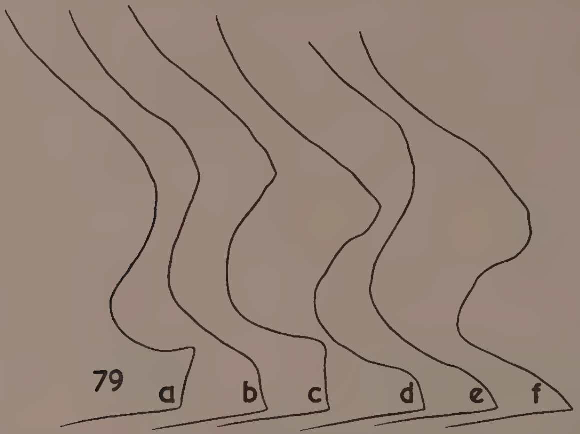

FIG. 79.—*Ceratophyllus styx jordani* Smit. Outlines of sternum VII of female, from Dyce, Aberdeenshire (*a* and *b* from one nest, *c*–*f* from another).

Description.[6]

C. styx jordani subsp. n. (figs. 75–79).	*C. styx styx* Rothschild, 1900 (figs. 71–74).
Holotype male and allotype female, ENGLAND: Tring, Herts., from nest of *Riparia riparia* vii.1907 (*N. C. Rothschild*). Paratypes: 7 ♂, 13 ♀ with same data as holotype and allotype; 1 ♂, Tring, *Riparia riparia*, viii.1900 (*N. C. Rothschild*); 1 ♀, Wilstone Reservoir nr. Tring, taken off *Riparia riparia*, 19.vii.1915 (*K. Jordan*).	Holotype male: ENGLAND: Lyndhurst, Hants, from [nest of] *Riparia riparia*, 11.vii.1900 (*G. Tate*).
Male.	*Male.*
Marginal spinelets of terga I–VI, on both sides together: 6·6, 8·1, 7·8, 7, 5 and 2·7 respectively (total 37·2).	Marginal spinelets of terga I–VI, on both sides together: 5·3, 7·6, 7·4, 6·4, 4·7 and 2·5 respectively (total 33·9).
Tergum VIII (fig. 76) broad, its dorsal margin behind the sensilium almost straight; area spiculosa 1·7 times as long as high.	Tergum VIII (fig. 72) narrower, its dorsal margin behind the sensilium usually convex; area spiculosa 0·9 times as long as high (or 1·1 times as high as long).

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[6] The numbers of the marginal tergal spinelets given are the means of counts on 25 specimens; all measurements given in the descriptions are means of the measurements of nine specimens.

Sternum VIII (fig. 75): ratio of length of proximal widened part (measured to the small arrow on fig. 75): length of narrow distal arm = 1 : 1·8. Ratio of height of proximal part : length of proximal part = 1 : 1·5. Relatively and actually the proximal part is shorter than that of *C. styx styx*, while the distal arm is much longer (cf. fig. 71).	Sternum VIII (fig. 71): ratio of length of proximal widened part (measured similarly): length of narrow distal arm = 1 : 1·2. Ratio of height of proximal part : length of proximal part = 1 : 2.
Manubrium of clasper (fig. 75) 2·38 times as long (measured along the dorsal margin) as wide in its middle.	Manubrium of clasper (fig. 71) 2·53 times as long (measured similarly) as wide in its middle.
Process P of clasper (fig. 75) broad, with a feebly oblique apical margin, below which the posterior margin is slightly incurved; the two acetabular setae are inserted at a much higher point than in the nominate subspecies (cf. fig. 71).	Process P of clasper (fig. 71) narrower (the corpus of clasper is also less stout), with an oblique apical margin, below which the posterior margin is markedly incurved.
Movable process of clasper wide, 1·8 times as long as its maximum width.	Movable process of clasper narrower, 2·7 times as long as its maximum width.
Apical lobe of distal arm of sternum IX (fig. 75) 2·3 times as long as its maximum width, the basal half of its ventral margin strongly convex and the apical half concave; apical portion wider than in *C. styx styx*.	Apical lobe of distal arm of sternum IX (fig. 71) 3·9 times as long as its maximum width, its ventral margin straight for the greater part of its length; apical portion narrow.
Apex of aedegal crochet fairly narrow and tapering to a blunt point (fig. 77).	Apex of aedeagal crochet broad and rounded (fig. 73).
Female.	*Female.*
Marginal spinelets of terga I–V, on both sides together: 6, 7·7, 6·8, 5·6, 2·1 respectively (total 28·2).	Marginal spinelets of terga I–V, on both sides together: 5·7, 7·6, 6·8, 5·3 and 2·6 resp. (total 28).
Sternum VII (fig. 78*a–d*) with a broad ventral lobe, above which the margin is deeply sinuate but specimens from near Aberdeen show a remarkable range of variation (fig. 79*a–f*) and the extreme form (*f*) resembles sternum VII of *C. r. riparius* (occurring in North America and Eastern Transbaikal.)	Sternum VII (fig. 74 *a–f*) without such a prominent ventral lobe, but with a rather variable lateral lobe below which the margin may be either straight or concave.
Distribution.[7]—ENGLAND: Tring (Herts); Lyndhurst (Hants); St. Leonards (Sussex); Moulton, Oundle (Northants); Rothley (Leics); Stiffkey (Norfolk); Alderley Edge (Cheshire); Radcliffe (Lancs); Blaydon (Durham); Great Salkeld (Cumberland). WALES: Llanedeyrn (Glamorgan); Tenby (Pemb).	*Distribution.* — ENGLAND: Lyndhurst (Hants); St. Leonards (Sussex); Reigate (Surrey); Wareham (Dorset); Putney (London); Stanstead, Harlow (Essex); Radlett (Herts); Haw Bridge (Glos); Radcliffe (Lancs); Oulton Broad (Suffolk); HOLLAND; BELGIUM; LUXEMBURG; FRANCE; GER-

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[7] Based upon specimens in the Rothschild and British Museum collection at Tring and upon material kindly lent by several colleagues; see map, fig. 82, on p. 362 of this volume.

Scotland: Grantshouse (Berwickshire); Morningside (Midlothian); Cullalo Hills, Dunbarnie (Fifeshire); Perth (Perthshire); Denmore, Dyce (Aberdeenshire); Tongue (Sutherland); Monifieth (Angus); Eckford (Roxburghshire). Ireland: Holmpatrick (Skerries: Dublin).

many; Denmark; Central Sweden; Poland; Austria; Switzerland; Czechoslovakia; Russia: Moscow area, Stavropol region and Kazakhstan.

Specimens which are intermediate between *s. styx* and *s. jordani* have been found at Lyndhurst (Hants); Hawbridge (Glos); Oxford (not marked on the map, fig. 82), and Stiffkey (Norfolk).

N. C. Rothschild (1909 : 57) described a female of the continental subspecies under the name of *Ceratophyllus flaveolus*, not realising (because it came from an accidental host, *Mustela erminea*) that the specimen he described was the sand martin flea, and he compared it with *Ceratophyllus gallinae*; its sternum VII is like fig. 74*e*. The name *Ceratophyllus flaveolus* Rothschild, 1909, is a synonym of *Ceratophyllus styx styx* Rothschild, 1900.

THE DISTRIBUTION OF *CTENOPHTHALMUS NOBILIS* AND *CERATOPHYLLUS STYX* IN BRITAIN.

> "*It is distressing not to know the right answer to an important question, and only to be able to venture a guess.*" Jordan (1938).

Ctenophthalmus nobilis

The distribution of *C. nobilis* in Britain is of great interest—a fact that is in no way affected by the question of its specific or subspecific status. At the present time *C. nobilis*, and in fact the whole *agyrtes*-complex (or superspecies) parasitises a wide range of small mammals including Voles (Microtinae), Field Mice (Murinae) and Shrews and Moles (Insectivores). *C. nobilis*, however, is found commonly on *Apodemus fridariensis* (Kinnear)[8] on Fair Isle (the only small mammal on the island) and in the Hebrides and Ireland where Voles are absent. This strongly suggests that the original hosts of *C. nobilis* were Long-tailed Field Mice of the genus *Apodemus*.

Furthermore, the fact that *C. nobilis* is found on Fair Isle strongly suggests that it is an early colonist. The position and date of the various land connections that at one time existed between the mainland of Britain and the various outlying islands are still open to discussion, but one of the few theories that are now generally accepted is that the Shetland Isles, including Fair Isle, have not been connected with the mainland during the Holocene period. There was almost certainly a land connection to these islands following the second glacial phase, since it is inconceivable that the ancestors of *A. fridariensis* would have survived the severe second glacial phase on Fair Isle. It is thought (Beirne, 1952 : 98) that *A. fridariensis* reached Britain during the first interstadial, but was not isolated on Fair Isle until the second interstadial (of the fourth glaciation). Subsequently Britain was invaded from the Continent by two species of Long-tailed Field Mouse, *A. flavicollis* (Melchior) which is absent from Ireland and Scotland, and the Holocene colonist *A. sylvaticus* (L.), which is present as far north as the Orkneys and occupies the whole of Ireland, but is absent from the Hebrides and various western islands off the coast of Scotland (see fig. 84).

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[8] In the most recent catalogue of Palaearctic mammals (Ellerman and Morrison-Scott, 1951) *Apodemus fridariensis* is regarded as a subspecies of *A. flavicollis* and *A. hebridensis* as a subspecies of *A. sylvaticus*. They have been called species in this discussion purely as a matter of convenience.

It must be assumed that these mice brought their fleas with them. There is a fairly large area in the north-west and centre of France (see fig. 81) where *C. nobilis* is found to-day, and it is possible but unlikely that it was far more widely distributed in the past, and was in fact the only flea of the *agyrtes*-complex parasitising both *A. flavicollis* and *A. sylvaticus* when they spread northwards into Britain as the ice sheets receded. It seems far more reasonable to postulate that the endemic flea *C. nobilis* was better adapted to the climatic conditions in Britain and passed successfully from its hosts on to both *A. flavicollis* and *A. sylvaticus*, at the expense of their own fleas. This situation is exactly the reverse of that which we appear to find in the case of *C. garei* and *C. borealis*, where the invading flea (*C. garei*) carried northwards on a wide variety of hosts, has apparently competed successfully with the resident population, and replaced it in all but a few isolated areas.

It is to be assumed that one of the later waves of *A. sylvaticus* was responsible for the introduction into Britain of the subspecies *C. n. nobilis*, which had meanwhile become differentiated in eastern and central France. This is discussed below (p. 360). It is more difficult to account for the isolation of *C. nobilis* in France. If we assume that *C. nobilis* (or its ancestors) occupied Britain as a parasite of the ancestors of *A. fridariensis* and *A. hebridensis* (de Winton) it must, with its hosts, have been driven southwards in front of the extending ice-sheets of the severe second glacial phase. It probably took refuge in the extension of ice-free land that existed west and south-west of the British ice-sheets as far south as the north coast of Spain (Beirne 1952, Moreau 1954). There is evidence that mammals from Britain, together with their fleas, retreated as far south as northern Spain, since recently Dr. Dunnet has made the interesting discovery (1955 : 447) that *Peromyscopsylla silvatica spectabilis* (Roths.), previously known only from Britain, occurs in the Cantabrian Mountains in northern Spain. It is also worth noting that *Ctenophthalmus agyrtes hispanicus* Jordan[9] is very closely related to *C. nobilis*. Some unknown isolating factor must obviously have kept the populations of *C. nobilis* and *C. a. hispanicus* apart from the rest of the *agyrtes*-complex. Maybe a clue is to be found in the fact that in the southern part of its range to-day *C. agyrtes* is a flea of temperate or cold zones. This was recently confirmed by Peus (1954 : 125), who found *agyrtes* subspecies in Greece only at high altitudes and not in the low-lying valleys between them. It is possible that *C. agyrtes* was, during the warmer periods of the long interstadials, confined to the Alps and the surrounding areas. Beirne (1952 : 47) also draws attention to the fact that " The existing British population of a glacial-phase survivor may therefore be the descendant of representatives of two or more populations that invaded these islands during different glacial phases . . . the descendants of the various invasions were able to interbreed. For this reason it is normally impossible to say whether a

[9] F. G. A. M. S. considers that on morphological grounds *hispanicus* could well be accorded specific rank ; it is much closer to *nobilis* than to the rest of the *agyrtes*-complex.

glacial-phase survivor is the survivor of one or several invasions". The same must to a certain extent apply to early interstadial survivors that, on the expansion of the ice-sheets, retreated to the same general areas in the south. Thus the ancestors of *C. nobilis* may have been driven back into the area of its distribution in France more than once—perhaps eventually reintroduced after it had acquired at least some morphological distinction in Britain.

The discovery (F. G. A. M.S.) that *C. nobilis* is separable into two subspecies

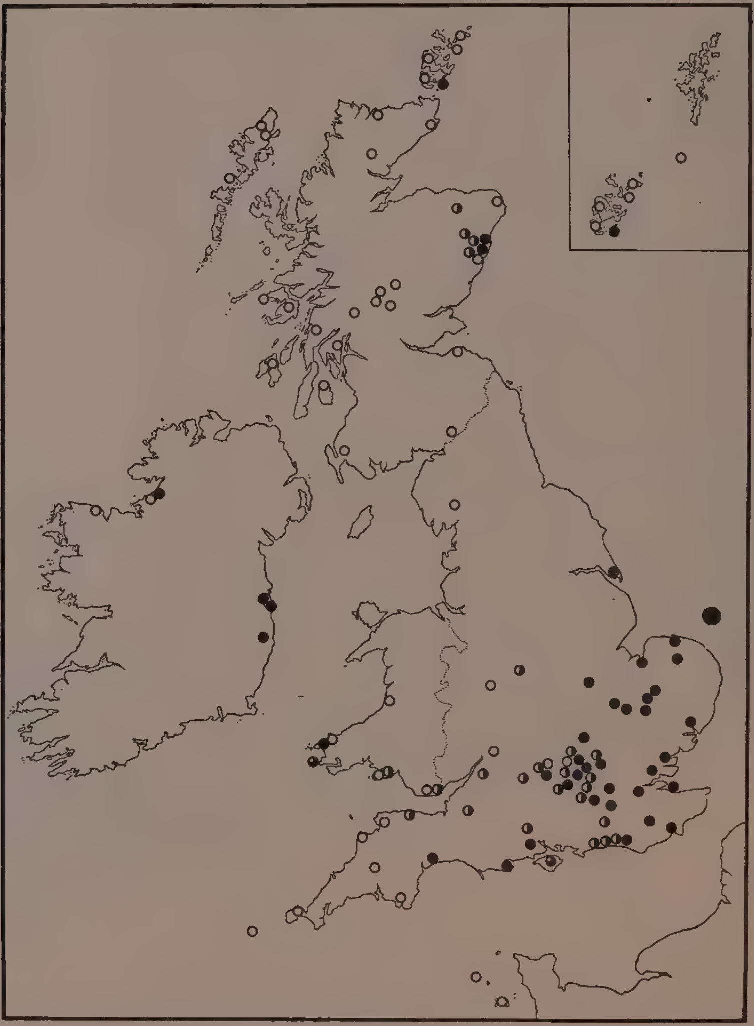

Fig. 80.—The distribution of *Ctenopthalmus nobilis nobilis* (●), *C. n. vulgaris* (○), and intermediates ◑ between *C. n. nobilis* and *C. n. vulgaris* in the British Isles.

is rather surprising. Their distribution is shown in figs. 80, 81. It will be seen that *C. n. nobilis* has its centres of distribution in the east and south-east of England, but also occurs on the east coast of Scotland (Aberdeen area), one of the Orkney Isles, the south-west corner of Wales and on both east and west coasts of Ireland. There is only one area in France where the subspecies has been collected. One of us (M. R.) found it at Royat les Bains (Puy-de-Dôme) on *Apodemus sylvaticus*, *Clethrionomys* sp. and *Sorex* sp. Collecting in France,

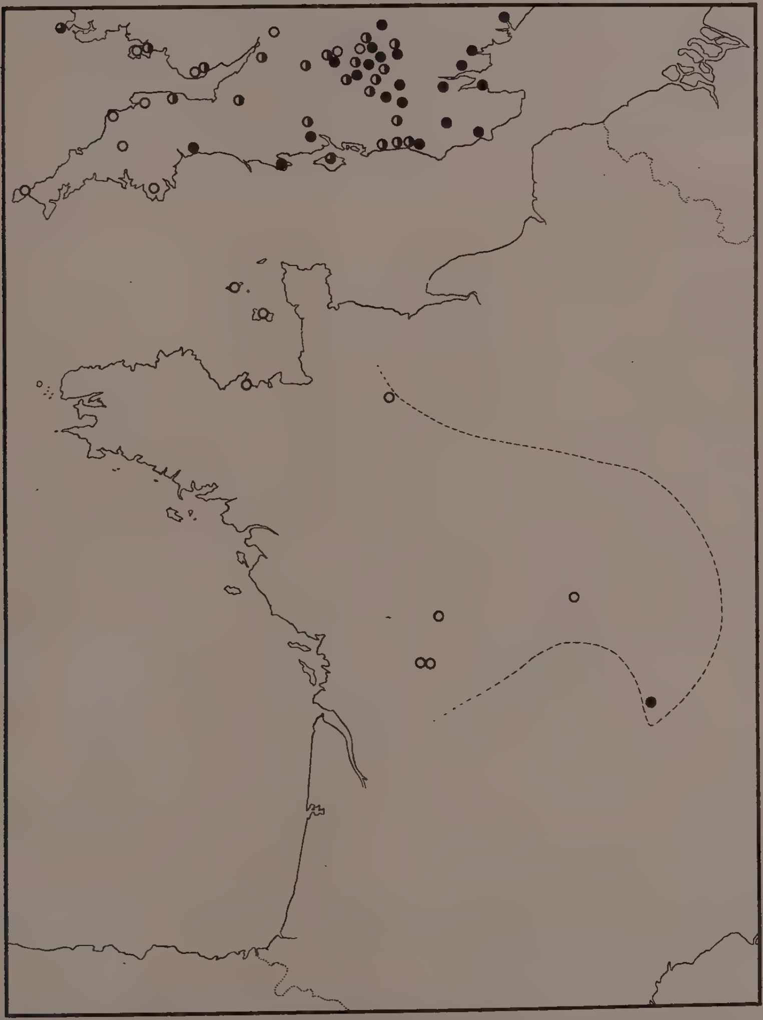

FIG. 81.—The distribution of *Ctenophthalmus nobilis nobilis* (●), and *C. n. vulgaris* (○) in France. The broken line demarcates the probable area of distribution of the species in France.

especially in the east, has been meagre, but this subspecies must be expected to occur in eastern France—how far east one can only guess. Intermediates occur in Britain where the two forms meet. This subspecies is absent from those islands, such as Fair Isle and the Hebrides, which are known to have been long separated from the mainland. There is, unfortunately, no relevant material available from north-east England beyond the Humber, but it seems probable that *C. n. nobilis* is distributed further northwards along the east coastal districts.

The distribution of *C. n. vulgaris* is altogether more westerly ; it occupies the Western Isles and the Highland areas of Scotland, north Scotland, Fair Isle, the Scillies and the Channel Isles. It has certainly been in Britain longer than the nominate form, and was probably sufficiently long isolated here to develop subspecific characters. A possible explanation—which is nothing more than a guess—is that the subspecies *C. n. nobilis* was introduced into Britain with one of the later Holocene colonisations by *A. sylvaticus*, at a period when, however, a land connection still existed between Ireland and the mainland (Beirne, 1952 : 144).

The curious distribution of these subspecies in Britain and the erratic zone of interbreeding may possibly be explained by the influence of present-day climatic factors. It will be seen that the centres of distribution of *C. n. nobilis* (with the exception of that of the east coast of Scotland) correspond with the area of lowest average rainfall (fig. 83), highest average temperatures and lowest altitude. Nowhere is it recorded from above 1500 feet. On the other hand, *C. n. vulgaris* is present in areas of maximum average rainfall, notably the west of Scotland, with lower average temperatures and frequently at relatively high altitudes (e.g. Benmore, Argyllshire, 2433 feet). Such factors may well restrict the range of the later invader, *C. n. nobilis*, by according definite advantages to *C. n. vulgaris* in these wetter, colder and higher localities.

It must be stressed that at the present time in Britain host preference appears to play no part in the distribution of the subspecies of *C. nobilis*. As we have noted, this flea parasitises a variety of small mammals, and its choice of host is probably governed by the requirements of the larval stages and the nests most suited to them. In order to understand the distribution of species that are not confined to one host a distinction should probably be made between the role of the host in (*a*) dispersal (or long-range distribution) and (*b*) distribution. The hosts which transport the adult flea are no doubt of paramount importance in the first instance, but of relatively little significance in the second. The adaptations of the larval stages, which are exposed to environmental factors equal in severity to those experienced by free (non-parasitic) insects, must exercise a much greater effect where we are concerned with local or small-scale distribution of subspecies.

There is another rather interesting, if puzzling, aspect of the distribution of the two subspecies of *C. nobilis*. The main morphological differences between subspecies of the whole *agyrtes*-complex are : (*a*) the shape and structure of the ventro-lateral aedeagal lobe ; (*b*) the shape of P^2 of the clasper, and (*c*) the width of the distal arm of sternum IX. It might seem reasonable to assume that a simple, non-sinuate P^2 is more primitive than a sinuate one, and also that the non-folded aedeagal lobe and the broader arm of sternum IX are more primitive than the folded lobe and the narrow arm. The subspecies with a smooth downwardly-bent aedeagal lobe, a non-sinuate P^2 and a broad arm of sternum IX occupy a central position both structurally and geographically. Moving from this centre outwards in all directions we find that the aedeagal lobe becomes " scaly " and eventually folds up where it reaches the outer margin of the area of distribution, P^2 becomes sinuate and the arm of sternum IX narrow. Thus on the fringe of the area occupied by *agyrtes* we find subspecies that are characterised by a folded aedeagal lobe and a deep sinus in P^2, for example : *C. a. provincialis* Rothschild (S.E. France), *C. a. wagnerianus* Peus (N.W. Yugoslavia), *C. a. graecus* Jordan (Greece, Bulgaria), *C. a. eurous* Jordan & Rothschild (Rumania) and *C. a. kleinschmidtianus* Peus (Russia). In *Ctenophthalmus nobilis* we find a folded aedeagal lobe, although the surface structure is somewhat different (see p. 346). The subspecies that occurs on the western side of France and Britain is characterised by a sinuate P^2, while the subspecies in the east, which is geographically nearer the centre of the distribution of the *agyrtes*-complex, has a non-sinuate P^2. It would be easier to understand this distribution if we could assume, on the contrary, that the sinuate P^2 characterises a more ancient form persisting to-day in marginal areas, and that the non-sinuate form characterises a more recent invading population. Again, it must not be forgotten that insects frequently exhibit special characteristics at the edges of their ranges, and it is possible that the sinuate P^2 is associated with some invisible, but primarily ecological, adaptation. It is obvious that before we can hope to explain this distribution and abandon these flights of fancy for something approaching fact, we shall require more material, in the first instance from central and eastern France.

Ceratophyllus styx

The population of *Ceratophyllus styx* in Britain is divided into two well-defined subspecies. One of these subspecies (*C. s. jordani*) occupies the north and the midlands of England, Wales, Scotland and Ireland, and up to now has been found nowhere else in Europe ; the other (*C. s. styx*) the south, south-east and east midlands of England (fig. 82). Their areas of distribution meet and intermediates have been found at Lyndhurst, Hampshire ; Hawbridge, Gloucestershire ; Stiffkey, Norfolk and Oxford. It should be noted that we have seen a solitary female specimen of *C. s. styx* from Radcliffe, Lancs., and the typical northern form has been collected at two localities near the south coast. The southern nominate subspecies is found on the continent of Europe in France, Belgium, Luxembourg, Switzerland, Holland, Denmark, Germany, Austria, Czechoslovakia, Poland, central Sweden, Kazakhstan and the Moscow area.

In north-east Sweden, Finland, Transbaikalia and the U.S.A. the Sand Martin (*Riparia riparia riparia* (L.)) is parasitized by a very closely related flea, *Ceratophyllus riparius* Jordan & Rothschild, 1920. This breaks up into two subspecies, *C. r. freyi* Nordberg, 1935, in north-east Sweden and Finland, and *C. r. riparius* in Transbaikalia and U.S.A. Dr. Jordan, after comparing the mounted material available at Tring, decided on morphological grounds that " *C. styx* and *C. riparius* are two rather abruptly different species " (letter dated 6th November, 1950)—a point of view with which we concur.

It is generally agreed that parasites evolve at a slower rate than their hosts, since their environment is usually much more stable and less liable to the

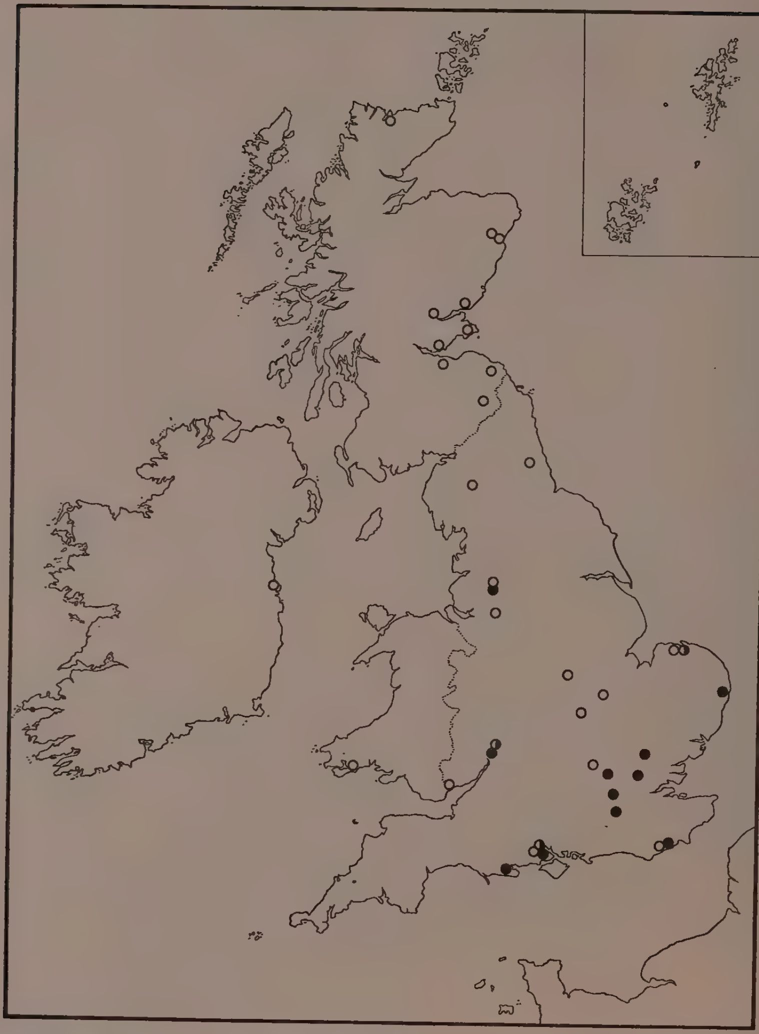

Fig. 82.—The distribution of *Ceratophyllus styx styx* (●) and *C. styx jordani* (○), and intermediates (◑) between *C. s. styx* and *C. s. jordani* in the British Isles.

violent fluctuations experienced by "free" animals, though Manter (1955), discussing the zoogeography of trematodes of marine fishes, says: "It should not be concluded that such is always the case, as there are examples of approximately equal divergence of both." One of us (Rothschild and Clay, 1948[10]) pointed out that in the case of the fleas of the Sand Martin (*Riparia riparia*), the host which migrates is less subject to the extremes of climate than the larval stages of the parasites that overwinter in the nest. Of the many hundreds of adult fleas present in a Sand Martin's nest only a relatively small proportion ever leave the burrow.[11] They obtain blood meals while the female incubates and while the young are in the nest, but remain behind when the nestlings are fledged. From the point of view of the speed of evolution these fleas may be regarded as free (non-parasitic) insects, and it is not really remarkable that they show subspecific or even specific distinctions while the host over the same area remains morphologically indistinguishable. There is, however, another possible explanation. At least four populations of Sand Martins must have been to some extent isolated from one another in the past—the two species (four subspecies) of flea referred to above are evidence of this. It is also possible that during this period the Sand Martin developed subspecific distinctions which have since been obliterated by subsequent contact and widespread interbreeding between the races involved; in this case the parasites would be, as usual, lagging behind and not going ahead of their hosts.

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[10] In this publication the authors suggested that *Ceratophyllus riparius* had evolved since the Sand Martin invaded the U.S.A. The discovery of *C. r. riparius* in Transbaikalia proves this is not so, but indicates that the American Sand Martins originated at

The distribution of the two subspecies of *C. styx* in Britain is interesting—despite the many lacunae due to lack of collecting. If we compare the area occupied by *C. styx styx* with maps (fig. 86) selected to illustrate the distribution of typical holocene colonists (Ford, 1955) such as the Oak Hook Tip Moth (*Drepana binaria*) or the Cream Spot Tiger Moth (*Arctia villica*) and Scarlet Tiger Moth (*Panaxia dominula*), it will be seen that they have much in common. Furthermore, the distribution of *C. s. jordani* is very similar to that of glacial phase survivors (fig. 85) (Beirne, 1952), such as the Smoky Wave Moth (*Pylarge fumata*) and the Juniper Carpet Moth (*Thera juniperata*).

The moth *Bupalus piniarius* (The Bordered White) has a somewhat similar distribution in Britain to *C. styx* (Cockayne 1912–13, Ford, 1955). Two forms of the moth occupy Great Britain, a small, paler Scandinavian race in northern England and Scotland, and a larger, more ochreous race in southern England. The two types meet and produce a variable hybrid population along a narrow zone somewhere about the level of Shropshire and Cheshire in England. Cockayne suggests that the Bordered White is an interglacial (= interstadial) relict in the north and a Holocene invader in the south, and that the two have extended their ranges and met since the retreat of the ice. In the case of *C. styx* the typical northern subspecies occurs in Ireland, whereas *Bupalus piniarius*

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any rate from the west. The race of Sand Martins present in Transbaikalia is not *Riparia r. riparia*, the subspecies present in both North Siberia and North America, but *R. r. ijimae* (Witherby, 1938). We do not know the subspecies of flea on *R. r. riparia* in North Siberia, but it will probably be *C. r. riparius*.

[11] Since going to press, Mr. F. A. Bak has kindly sent us a small collection of *C. styx* obtained from Sand Martins trapped in a colony in Leicestershire and "de-loused" by the Williamson chloroform method. Four recently-fledged juveniles trapped on the 3rd June, 1954, were found to harbour 16, 7, 2 and 5 fleas respectively, and five adults and two juveniles trapped on the 11th June, 1954, harboured 4, 1, 4, 2, 2, 3 and 2 fleas respectively. Mr. Bak has also given us the following very interesting information: he and Mr. Hickling have found that not only are old holes in the spring alive with fleas, especially after two or three days' warm weather, but also new nests established in a virgin sand face very quickly show a heavy infestation.

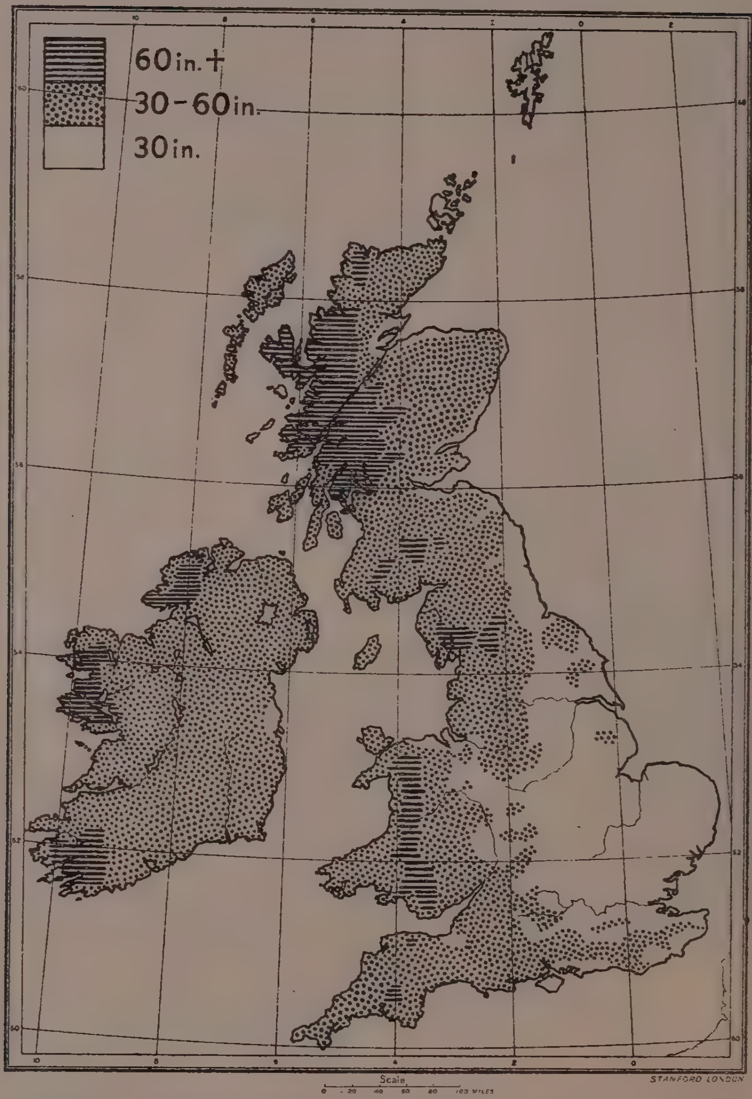

FIG. 83.—Average annual rainfall in the British Isles. After Beirne, 1952.

is represented by a rather distinct form in Ireland (Cockayne, letter dated April, 1955). The distribution of two wood ants, *Formica rufa* and *F. lugubris* (Yarrow, 1955, map on p. 12), is also somewhat reminiscent of that of the two subspecies of *C. styx*. *F. lugubris* occurs in the north of Scotland, southern Ireland, northern England and Snowdonia, whereas *F. rufa* occupies southern England and occurs somewhat sporadically in the Midlands and is also found

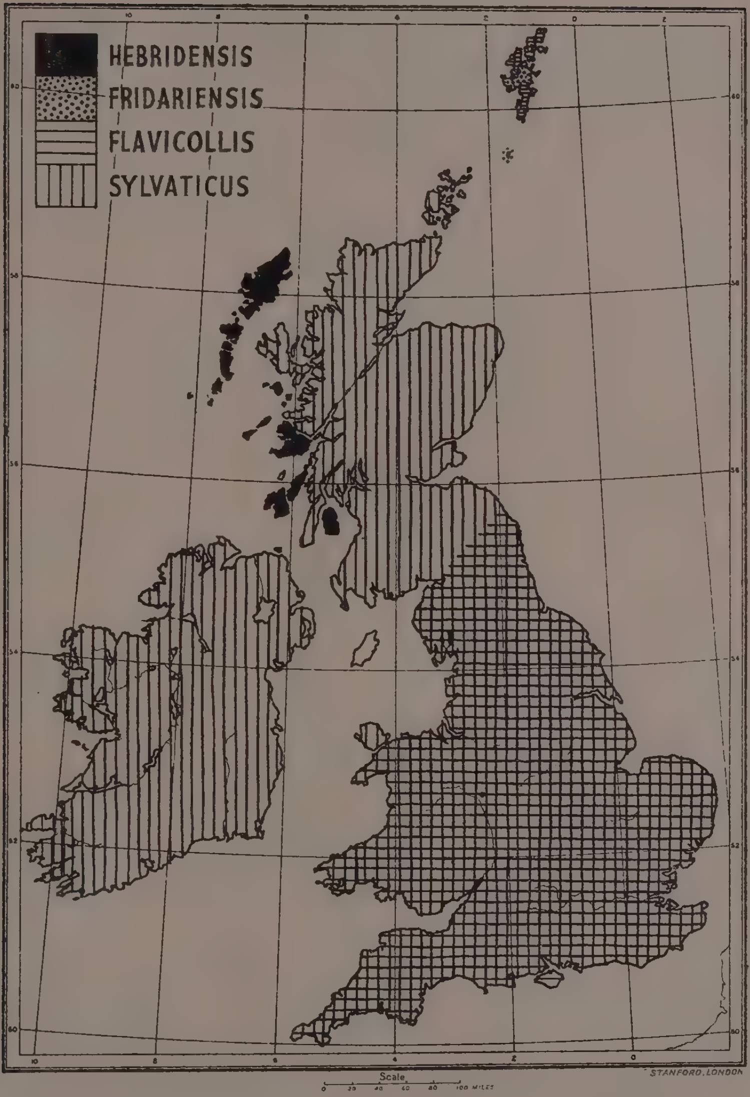
HEBRIDENSIS
FRIDARIENSIS
FLAVICOLLIS
SYLVATICUS
Scale
100 MILES
STANFORD, LONDON

FIG. 84.—The distribution of Long-tailed Field Mice (*Apodemus* spp.). After Beirne, 1952.

here and there throughout Wales (except Snowdonia). It will be noted that in this case the northern form occupies Ireland, but here we are dealing with two distinct species, and Yarrow states that in his experience: " *rufa* never does occupy territory sufficiently close to that of *lugubris* to make hybrids even a remote probability ".

The simplest explanation to account for the distribution of the two subspecies of *C. styx* is to postulate two separate colonisations of Britain by the Sand Martin. During the advance of the ice, in one of the glacial phases, the resident population of Sand Martins would have taken refuge on the Celtic land (the extension of ice-free land that existed west and south-west of the British ice-sheets (Beirne 1952 : 40, Moreau 1954 : 415)) and remained there in breeding isolation until they spread outwards again on the retreat of the ice to re-occupy the British Isles. During this period of isolation subspeciation of *C. styx* would have occurred. A second population of Sand Martins spread northwards during the Holocene to occupy southern England, bringing *C. s. styx*, which had evolved on the continent of Europe, with them.

Unfortunately, little is known about the past history or present migrations of the Sand Martin (Witherby 1938, Moreau 1954). One would have expected to find the British subspecies of *styx* in northern Scandinavia and along the northern fringe of Europe, in the same way that one finds *Ceratophyllus borealis*, *Bupalus piniarius* and *Formica lugubris* in this area. However, it is the rather distinct species *Ceratophyllus riparius* which is found here, and one must assume that the Sand Martin population (*Riparia r. riparia*) now breeding along the northern fringes of Europe (north-east Sweden and Finland), Siberia and portions of the U.S.S.R., must have originated from a different area or have been long isolated from those that now occupy the rest of Europe. Perhaps, like the Greenish Warbler (*Phylloscopus trochiloides viridanus* Blyth) or Eversmann's Warbler (*Phylloscopus borealis borealis* (Blas.)) they spread into these areas from the east, bringing *C. riparius* or its ancestors with them. But we simply do not know. One of us (Rothschild, 1952) has already indicated that the distribution of the fleas of the Hirundidae suggests that there may be a more or less permanent segregation and isolation of certain colonies and populations of these birds within the same areas of distribution. Do the Sand Martins from northern and southern Britain, for instance, winter in the same countries abroad ? Again we do not know. It is also possible that the Sand Martins (*Riparia r. riparia*) occupying the continent of Europe may be only apparently uniform. During their isolation (while the subspecies *C. s. styx* evolved) they would of necessity have become adapted to their environment, but possibly in ways that are not reflected in visible characters. Thus the presence of the two subspecies of *C. styx* in Britain would provide the only morphological evidence of these adaptations, which nevertheless keep the two populations of birds apart.

We do not, however, think it necessary to postulate either a double invasion or two discrete populations of the Sand Martin in Britain to-day to account for the distribution of the Continental subspecies of *C. styx* in southern and eastern England.

A most striking phenomenon observed by entomologists in recent years has been the rapid extension of their ranges—especially northwards—of a variety of British insects. For obvious reasons such extensions of range are most frequently recorded in conspicuous and well-collected groups such as butterflies and moths. However, one House Martin flea, *Ceratophyllus rusticus* Wagner, 1903, which at the beginning of the century was only recorded on very rare occasions, is now one of the most widely distributed and commonest species on this host in Britain. Ford (1945) remarks : " The explanation of these facts is decidedly obscure. . . . It seems almost certain that they are at least partly dependent on climatic effects, though none which can be correlated with them has ever been detected." A somewhat similar phenomenon appears to have occurred among birds. Lack (1954) has drawn attention to the spread northwards of the range of a number of species both in their winter quarters and breeding grounds, and has correlated this gradual change of range with climatic factors : " During the last 20 years a number of southern species have successfully colonised Greenland and Iceland or have spread north in Lapland. At the same time, various arctic species have become much scarcer in the south of their breeding range, including the Little Auk in Iceland and the Pine Grosbeak, Lapp Tit, Siberian Jay, and Whimbrel in Lapland. . . . As the Whimbrel has retreated north, so the closely related Curlew has spread north, which suggests that the two are in competition, the climatic factor determining the position of the boundary between them. . . . A particular group of small passerine species spreading north and north-west in Finland since about 1930 are all migrants which spend the winter outside Europe, mostly in the tropics and subtropics, and arrive on their breeding grounds in late May and early June. . . . Kalela has attributed their increase to the warmer weather that has occurred in June since about 1930, in which case their spread may well have been facilitated by the tendency, already discussed, for yearling birds to settle farther north than usual when their spring migration coincides with fine weather; but their persistence farther north has presumably been due to their finding conditions suitable for breeding."

Although ringing experiments have shown that adults of most species of birds normally breed where they bred in the previous year (Lack, 1954), yearling birds which take up their stations for the first time may breed further north than usual when their northward journey has taken place in unusually warm weather. In the case of the Sand Martin (Stoner, 1941) the proportion of adults that breeds in the same colony as in the previous year is much higher than the proportion of young birds that breeds in the colony where they were born. Taking all these facts into consideration it seems highly probable that numbers of young Sand Martins hatched and reared in northern France, Belgium, etc., seeking breeding stations for the first time, have from time to time extended their range slightly and filtered into southern England, intermingling with and inter-breeding with colonies along the south coast. This would have occurred especially while the land connection between Britain and the Continent still existed. In this way *C. s. styx* could have been introduced over and over again into these colonies, but possibly only in relatively recent times have the climatic conditions been sufficiently favourable to their larval stages to enable this subspecies to establish itself here and spread northwards. Fleas must be frequently carried beyond the range to which the temperature requirements of the larvae restrict them as a breeding species. Thus the adult of *Echidnophaga gallinacea* (Westwood), 1875, which is only able to breed in tropical or semi-tropical climates, has been recorded as far north as Britain on a migrating Wagtail (Thompson, 1952). Every autumn *C. styx* is carried southwards on migrating Sand Martins, and it appears highly probable that some fleas survive on their bodies until the following spring, when the birds migrate north again.

When the ranges of two subspecies meet the zone of hybridisation may be narrow—a mile or so across—or as wide as fifty miles. The two populations

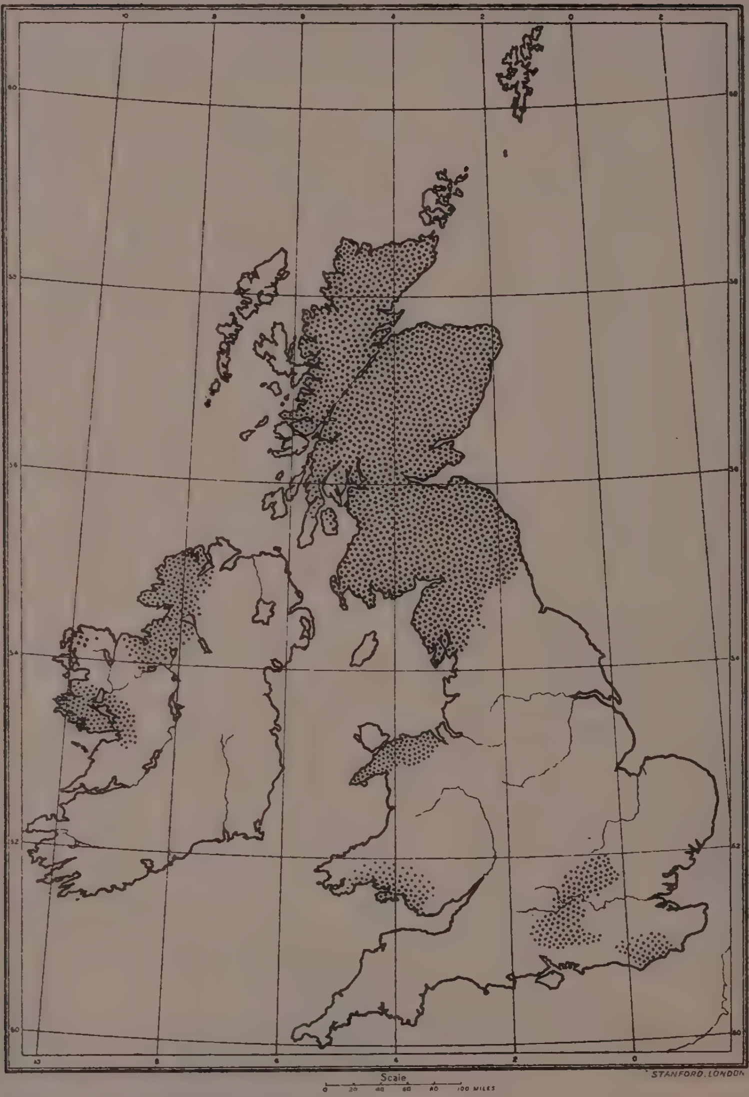
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Fig. 85.—The present range of a glacial phase survivor, the Juniper Carpet Moth (*Thera juniperata*). After Beirne, 1952.

exist as distinct subspecies on either side of this zone because, as Ford (1955) points out: "They have evolved independently and have each developed a gene complex adjusted to their needs, a mixture between which will, almost by definition, be less balanced than in either alone. Thus the hybrids even if freely produced will be at a relative disadvantage and therefore removed by selection, so preserving the pure forms intact in spite of their fusion."

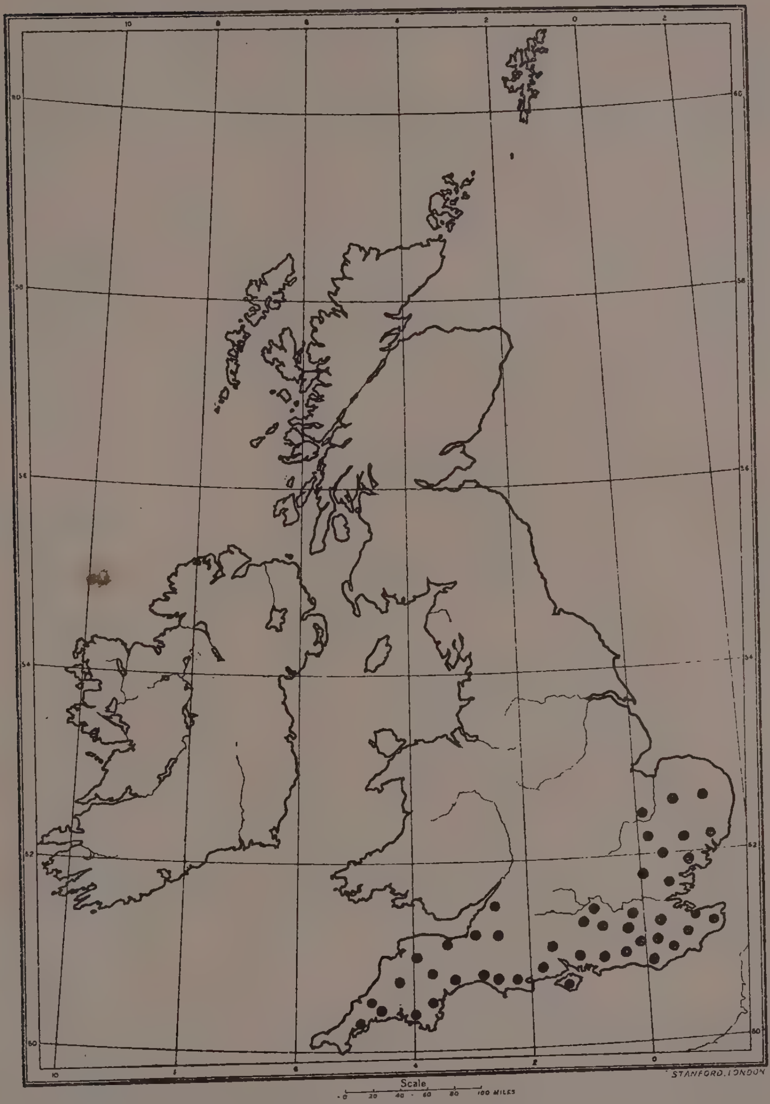

Fig. 86.—The present distribution of a holocene colonist, The Cream-spot Tiger Moth (*Arctia villica*). After Ford, 1955.

Mayr (1953) has also pointed out: "There is no zoogeographical barrier more formidable for a subspecies than the range of another subspecies." Nevertheless, this does not imply that, once two subspecies have extended their ranges and met, the zone of hybridisation must remain static. As the changing climatic effects favour one or other of the subspecies so their ranges will tend to expand or contract. Thus the zone of hybridisation, although probably remaining narrow, may be pushed further north or south as the case may be (it can even be broken up, as we have seen in *C. garei* and *C. borealis* (see p. 300 of this volume) and become a series of isolated patches). It seems quite probable that this is occurring in the case of *C. s. styx*, which may now be extending its range further northwards quite independently of any particular host movement.

The foregoing discussion is of necessity highly speculative. But there is just a slender chance that we may be able to test this last hypothesis during our lifetime. We have collections of *C. styx* from the Sand Martin at Ashton made during the early part of this century. These were the northern subspecies, *C. s. jordani*. Next summer we hope to examine further collections from the same colonies. Will these populations have changed during the last fifty years? During this period the Hornet (*Vespa crabro* L.), the Comma Butterfly (*Polygonia c-album* (L.)), the White Admiral (*Limenitis camilla* (L.)), the Buff Footman Moth (*Eilema depressa* Esper var. *unicolora*) and various other insects have extended their ranges as far north as Ashton. Shall we now find intermediates, or even *C. s. styx*, in the nests of the Sand Martin in this area?

The distributions of the three fleas from Britain described in this volume (p. 295, 341) have certain important features in common. In all three instances we are concerned with pairs of closely related fleas. The morphological differences between the subspecies of *C. styx* are such that little dispute could arise concerning their status as " good " subspecies. In the case of *C. garei* and *C. borealis* the differences are more pronounced and veer towards the specific, whereas the populations of *C. n. nobilis* and *C. n. vulgaris* appear to be distinguished by a single morphological character apparent only in the male.

The ranges of the subspecies (or species) of all three pairs meet at some points on the mainland of Britain and variable hybrids or " mongrels " are produced by interbreeding. If all the available evidence—distribution on the continent of Europe, the occupation of recognised areas of refuge (such as the Channel Isles, the Hebrides, Fair Isle, etc.), the hosts' distribution, habits and past history when these can be deduced, and present and past climatic conditions —is taken into consideration it seems possible that in all three cases we are dealing with interstadial survivors that are to-day at different stages of retreat before a later (probably Holocene) invader driving northwards and westwards from a centre on the continent of Europe. It seems likely that climatic factors acting upon the larval stages, which are free in the nest, have an important effect upon the spread and range of the subspecies concerned. The relationship with the hosts, so different in all three species, seems to exert little influence upon their present distribution in Britain. It appears at first sight that its predilection for the Wheatear might have some effect on the distribution of *C. borealis*, but the hole-nesting habits of this bird, coupled with its association with upland moorland both on the mainland and on inaccessible islands, has *destined* it to be left temporarily as a favoured host. But *C. garei* has already been found in the Wheatear's nest hybridising with *C. borealis*, so there has been insufficient isolation in this habitat to allow adaptation to proceed far enough to prevent or seriously hinder interbreeding. On the continent of Europe a different situation might develop at high altitudes. For instance, at Eigergletscher, Bernese Oberland (p. 310), *C. borealis* is breeding on the edge of the glaciers and the larvae must be exposed to very low temperatures when the birds are not occupying the nest. In such a habitat isolation might be prolonged, and eventually characters sufficiently distinct to prevent interbreeding may be, or have already been, developed.

In the foregoing paragraphs we have stressed the features which these distributions have in common, but they also present many aspects which are exceedingly obscure and for which we can offer no reasonable explanation. To draw attention to one only—the population of *C. n. nobilis* present on the east coast of Scotland.[12]

As we have already indicated, before we can hope to explain these distributions, much more collecting is necessary; thus we must try to trace the area in eastern France occupied by *C. n. nobilis*, the area in Switzerland occupied by *Ceratophyllus garei*, and discover whether the northern British subspecies of *C. styx* occurs in Spain and Portugal—at present we have no Sand Martin fleas at all from this area—and what subspecies is present on the bird in the Middle East and north-west India. But there seems little doubt that, in addition to collecting, breeding experiments will be required before the problem is solved satisfactorily.

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[12] The occurrence of *C. n. nobilis* around Aberdeen, in Ronaldshay (Orkneys) and at Bundoran (N. W. Ireland) might have been brought about by the introduction of rats and mice from S. E. England, e.g. by means of coasters.

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CONTRIBUTION À L'ÉTUDE DES HEPIALIDAE (31ÈME NOTE).[1] SUR QUELQUES SPÉCIMENS DU TRING MUSEUM.

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Avec 6 Texte-figures.

LES Hepialidae ne furent pas une des familles étudiées par le Dr. K. Jordan ; par contre Lord Rothschild en a décrit un certain nombre, particulièrement les espèces spectaculaires ; mais, comme le matériel étudié ici provient uniquement du Tring Museum, je ne crois pas déplacé de publier cette étude dans le livre jubilaire du Dr. K. Jordan.

La collection d'Hepialidae du Tring Museum, comme celle de toutes les autres familles, est fort riche, particulièrement en matériel sud-américain ; ma 25ème note a déja été consacrée à l'étude d'une partie de ce matériel (1951, *Ann. Mag. nat. Hist.* (12) **4** : 1272) ; celui étudié ici provient d'Afrique et d'Amérique du Sud.

Tous les types sont déposés au British Museum (Natural History).

Pour terminer cette introduction, je ferai connaître un moyen pratique pour monter en milieu épais les genitalia mâle ou femelle qui, comme souvent chez les *Hepialidae,* sont globuleux. Il suffit de couper avec une lame de rasoir, une allumette en quatre parties, dans le sens de la longueur, par deux coupes perpendiculaires. Les morceaux, coupés à la longueur voulue, seront, après un passage de quelques instants dans le xylol, placés dans le baume avec les genitalia et disposés latéralement avant de poser la lamelle. C'est là une méthode simple et rapide lorsque l'on ne dispose pas de lames concaves ou de cales en verre. Un baume un peu épais est à employer de préférence.

I. AFRIQUE.

Si le Dr. K. Jordan est connu comme l'un des plus grands lépidoptèristes, systématicien et descripteur, on le connait moins comme voyageur-récolteur. Les deux espèces décrites ci-dessous ont été récoltées par lui en Angola. A ma connaissance, peu de travaux, excepté ceux de Tams sur les Lasiocampidae (1936, *Novit. zool.* **40** : 95) et de Collenette, sur les Lymantriidae (*loc. cit.* : 147), ont été publiés à la suite de ce voyage dans cette intéressante région, fort peu connue, qu'est l'Angola.

Eudalaca jordani sp. n.

Envergure 26–21 mm. ; longueur des ailes antérieures 12–10 mm. ♀ plus grande que ♂. Antennes fauves. Tête noirâtre ; thorax, parsemé de poils noirâtres, comme l'abdomen, gris ocre pâle. Devant du corps, dessous du thorax et pattes gris noirâtre ; dessous de l'abdomen comme le dessus.

Ailes antérieures de couleur fondamentale gris ocre clair, avec deux taches, surtout la proximale, plus ou moins nettes, brunes et finement limitées latéralement de blanc ; la plus proximale subrectangulaire, oblique, du bord antérieur de la cellule à la nervure anale, au quart basal de l'aile ; l'autre, au niveau des discocellulaires, triangulaire, large au bord

[1] 30eme note : 1953, *Lambillionea* **53** : 32.

antérieur de la cellule et sur R5, avec la pointe se confondant avec la couleur fondamentale dans la région du tornus. Région costale, un peu plus gris foncé que le fond, présentaute 7–8 petites taches brun clair subcarrées, limitées latéralement de blanc sale. Frange de la couleur fondamentale.

Ailes postérieures brunes unicolores, avec le radius jaunâtre. Frange brune.

Dessous des quatre ailes brun.

Armure génitale mâle (fig. 1).

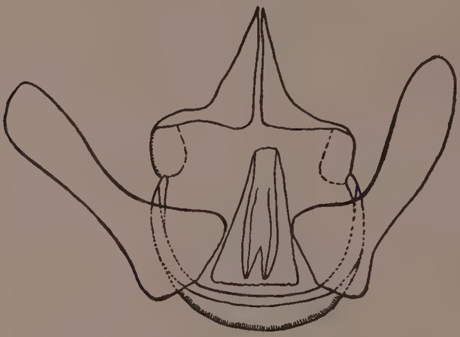


Fig. 1.—*Eudalaca jordani* sp. n., genitalia ♂.

Holotype ♂, allotype ♀, Angola : Mt. Moco, Luimbale, 1800–1900 m. ♂, 24.iii.1934 ; ♀, 18.iii.1934 (*Dr. K. Jordan*).

Paratypes : 2 ♂, même localité, 18.iii.1934 (genitalia ♂, prép. P. Viette, no. 2570) ; 24.iii.1934 (genitalia ♂, prép. P. Viette no. 2412). Tous les deux endommagés lors d'un voyage Paris-Londres.

L'espèce est voisine d'*E. minuscula* (Janse) et d'*E. onthocosma* (Janse) (1942, *Moths of South Africa*, **4** (1) : 22, 24 ; pls. 43 et 48), mais s'en distingue par l'absence de bande blanchâtre. Les valves présentent un fort lobe à la base ventrale ne se retrouvant pas chez les deux espèces citées.

Gorgopis libania **angolensis** subsp. n.

Envergure 36–41 mm. ; longueur des ailes antérieures 16–19 mm.

Se distingue par la couleur brun foncé des ailes antérieures, principalement, ne présentant pas de marbrures jaunâtres. L'aspect général des écailles n'est pas aussi grossier que chez les *libania* typiques.

Forme générale de l'armure génitale mâle étant bien celle de *libania*, principalement la courbure en angle droit des valves, mais le processus médian situé au bord dorsal du vinculum pointu, comme celui figuré par Janse (1942, *Moths of South Africa*, **4** (1), Pl. 52) pour *G. armillata* Meyrick (1921, *Ann. Transv. Mus.* **8** : 141), au lieu d'être large et tronqué comme chez les *libania* typiques.

Holotype ♂, Angola : Mt. Moco, Luimbale, 1800–1900 m., 18.iii.1934 (*Dr. K. Jordan*).

Paratypes : 5 ♂, même localité, 18 et 20.iii.1934 (genitalia ♂, prép. P. Viette no. 2989).

En, 1952, *Ann. Mag. nat. Hist.* (12) **5** : 869, Tams a décrit, sous le nom de *salti*, un *Gorgopis* nouveau du Kilimandjaro capturé à environ 4000 m.

d'altitude. Notons que deux *Gorgopis* d'altitude étaient déja décrits du Kilimandjaro, viz., *G. alticola* Aurivillius (1910, *Kilimandjaro-Meru Exped.* (Zool.), Abt. 9, p. 55) (2 cotypes au Muséum de Paris) capturé en grand nombre, entre 3000–4000 m. par la mission suédoise d'Y. Sjöstedt et *G. altitudinis* Le Cerf (1914, *Bull. Soc. ent. Fr.* **83** : 402) (type, Muséum de Paris) capturé également en grand nombre, entre 2600–2800 m. par la mission française de Ch. Alluaud et R. Jeannel. *Cf.* ma 2ème note (1947, *Rev. franç. Ent.* **14** : 22).

II. Amerique du Sud.

Paragorgopis nigrovenosalis sp. n.

Envergure 31 mm. ; longueur des ailes antérieures 15 mm.

Antennes gris jaunâtre, avec le scape noirâtre. Tête, pro- et mésothorax brun ocre, métathorax et abdomen jaune ocre. Pattes pro- et mésothoraciques, comme le dessous des mêmes segments, brun ocre, tarses prothoraciques brunâtres ; pattes métathoraciques ocre rougeâtre ; le dessous de l'abdomen comme le dessus.

Ailes antérieures de teinte ocre rougeâtre, surtout dans la partie proximale de la cellule, avec deux bandes parallèles à la marge externe, grisâtres dans la moitié distale ; région du bord inférieur grise, coupée de barres transversales plus foncées. Côte et marge externe finement noirâtres. Une longue strie longitudinale noire se trouve au milieu de la cellule au niveau des médianes. Frange gris rougeâtre.

Ailes postérieures ocre pâle, légèrement transparentes, bordées de noirâtre, avec une ombre longitudinale noirâtre comme aux antérieures, mais à peine marquée.

Dessous ocre, légèrement teinté de rougeâtre, avec l'indication de la strie longitudinale du dessus.

Armure génitale mâle (fig. 6).

Holotype ♂, Brazil : Minas Geraës, Aqua Suja, x.1906 (*E. A. Baer*) (genitalia ♂, prép. P. Viette no. 2990).

Cette espèce, par les deux parties latérales fortement sclérifiées, ne se rapproche d'aucune autre connue.

Paragorgopis spitzi sp. n.

Envergure 35 mm. ; longueur des ailes antérieures 17 mm.

Antennes, palpes labiaux, tête, thorax, abdomen, dessous du corps et pattes ocre rougeâtre.

Ailes antérieures de couleur fondamentale ocre rougeâtre, avec l'espace compris entre la côte, les nervures discoïdales et Cu 1 unicolore et plus foncé. A la base de M1 et un peu au-dessus, une petite tache dorée melée, sur son pourtour, d'écailles noires. Entre la cellule et la marge externe, deux bandes transversales de points noirâtres, situés entre les nervures et entourés d'une auréole de la couleur fondamentale plus foncée ; ces deux lignes se rejoignent dans la région du tornus, la plus externe moins marquée que l'interne ; cette dernière présente, au même niveau que celle de la base de M1, une petite tache dorée, reliée à la précédente par une petite ligne longitudinale noire. Le long de la marge externe une bande marginale de taches grises, chaque tache étant située entre les nervures. Côte légèrement noirâtre. Frange brun ocre.

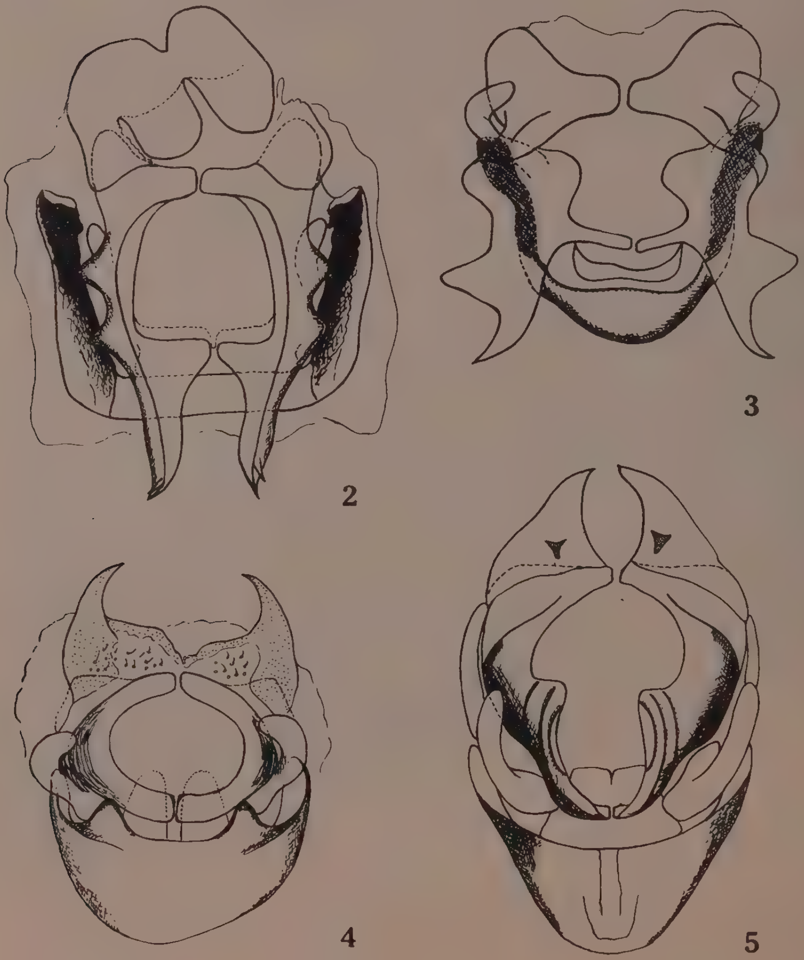
Ailes postérieures uniformément ocre rosé, sans aucun dessin, avec la frange comme aux ailes antérieures.

Le dessous des ailes ocre rosé avec une légère indication, aux antérieures, des taches du dessus.

Armure génitale mâle (fig. 2).

Holotype ♂, Brazil : São Paulo, Ypiranga, viii.1922 (*R. Spitz*) (genitalia ♂, prép. P. Viette no. 2297).

Cette espèce se distingue du groupe *pittionii* Vtt.-*foetterlie* Vtt. (1951, *Ann. naturh.* (*Mus.*) *Hofmus. Wien* **58** : 141) par la forme des processus du tegumen, qui présentent ici deux lobes saillants dans leur partie médiane et aussi par la présence de deux petites pointes à leur apex.



Figs. 2–5.—Genitalia ♂ de (2) *Paragorgopis spitzi* sp. n. ; (3) *P. jordani* sp. n. ; (4) *Xytrops pluriargenteus* sp. n. ; (5) *Schaefferiana simplex* sp. n.

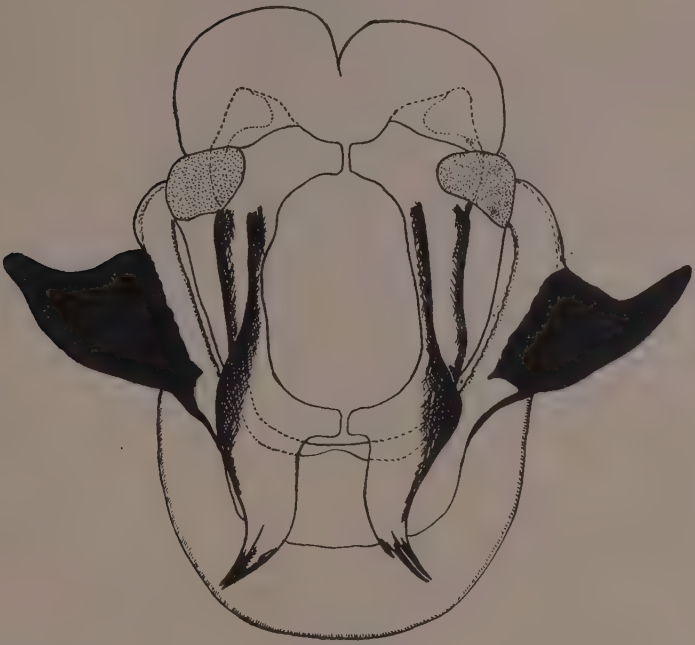


FIG. 6.—*Paragorgopis nigrovenosalis* sp. n., genitalia ♂.

Paragorgopis jordani sp. n.

Envergure 31 mm. ; longueur des ailes antérieures 14·5 mm.

Antennes, palpes labiaux, tête, thorax, abdomen, dessous du corps et pattes ocre légèrement brunâtre.

Couleur fondamentale des ailes antérieures ocre pâle. Côte brunâtre, avec quelques taches plus foncées dans la moitié apicale. On distingue à peine, comme dessins, deux bandes de taches transversales entre la cellule et la marge externe ; la plus interne faite de taches noirâtres, n'atteignant pas la côte et ne dépassant pas l'espace M1–M2, où elle rejoint une petite ligne longitudinale noirâtre venant de la cellule, les taches entourées d'ocre plus foncé que celui de la couleur fondamentale ; la bande la plus externe submarginale, faite de taches blanc jaunâtre entourées d'un liseré d'écailles noires. A la base du secteur radial, une courte ligne oblique et noire. Frange brun ocre.

Ailes postérieures uniformément ocre rosé, sans aucun dessin, avec la frange comme aux ailes antérieures.

Dessous des ailes ocre rosé, avec quelques indications, plus foncées, des dessins du dessus.

Armure génitale mâle (fig. 3).

Holotype ♂, BRAZIL : Minas Geraës, San Jacintho Valley, Theophilo Ottoni, 1907–8 (*F. Birch*) (Genitalia ♂, prép. P. Viette no. 2329).

Cette espèce est du même groupe que l'espèce précédente, avec les deux lobes latéraux externes des processus du tegumen plus saillants, plus développés (surtout le plus inférieur) et situés au tiers proximal et distal, mais ici les pointes apicales sont absentes.

Xytrops pluriargenteus sp. n.

Envergure 29–30 mm. ; longueur des ailes antérieures 16 mm.

Antennes brunes ainsi que les palpes labiaux, la tête et le thorax ; abdomen gris brun, avec une zone plus claire, médiane, dorsale sur chaque segment et les parties latérales gris rose ; dessous du thorax et pattes bruns ; celui de l'abdomen gris jaunâtre.

Ailes antérieures de couleur fondamentale grise. Espace costal avec une série de taches brunes. La cellule occupée en grande partie par une tache triangulaire brun fauve, avec, à la base, quelques petits points dorés et, au niveau des discocellulaires, trois taches dorées, la plus interne allongée et les deux autres plus petites superposées. En dessous de la cellule, l'aile de la couleur fondamentale plus claire sauf sur une zone oblique subrectangulaire, allant de la tache centrale à l'extrémité de la nervure anale. Entre les discocellulaires et la marge externe, deux bandes transversales brun roux ; la plus interne plus régulière, la plus externe, presque marginale, faite de taches situées entre les nervures ; dans la région apicale, ces bandes tendent à disparaître, par suite de l'envahissement du brun roux et elles se rejoignent au tornus. Une ligne marginale est faite de petites taches isolées, noirâtres, entourées de blanc jaunâtre. Frange brun roux.

Ailes postérieures brunes, avec la base plus claire et la zone marginale teintée de roux.

Dessous des ailes brun jaunâtre, avec quelques taches jaunes à la côte et une zone marginale aux deux ailes plus larges aux postérieures.

Armature génitale mâle (fig. 4).

Holotype ♂, Brazil : São Paulo, Alto da Serra, i.1923 (*R. Spitz*) (genitalia ♂, prép. P. Viette no. 2296).

Paratype : 1 ♂, même date.

Je rapporte aussi à cette espèce les deux exemplaires suivants :

1 ♂, Jaragua do Sol, Sta Catharina, i.1935 (*F. H. Hoffman*).

1 ♂, Ypiranga, S. Paulo, ii.1923 (*R. Spitz*) (genitalia ♂, prép. P. Viette no. 2380).

Cette espèce se différencie de l'espèce type du genre *monoargenteus* Viette (1951, *Bull. sci. Bourgogne* **13** : 2) et de *dorita* Schaus (1901, *J. N.Y. ent. Soc.* **1** : 76) par la présence des deux lobes latéraux au bord dorsal du vinculum.

Schaefferiana simplex sp. n.

Envergure 31 mm. ; longueur des ailes antérieures 14 mm.

Antennes jaunâtres. Tête, thorax et abdomen jaune ocre ; le dessous et les pattes de même couleur, mais plus clairs.

Ailes antérieures frottées, mais on distingue une couleur fondamentale jaune dorée avec une bande transversale oblique, blanche, partant de la côte un peu avant l'apex et atteignant le bord inférieur à l'apex de la nervure anale ; cette bande bordée intérieurement, entre chaque nervure, par une petite barre brune perpendiculaire.

Ailes postérieures légèrement rosées.

Le dessous jaunâtre.

Armure génitale mâle (fig. 5).

Holotype ♂, Brazil : Minas Geraës, San Jacinthe Valley, Theophilo Ottoni, 1907–8 (*F. Birch*) (genitalia ♂, prép. P. Viette no. 2991).

Espèce très proche d'*epigramma* Herrich-Schaeffer, mais s'en distinguent par les côtes et l'allure générale des processus latéraux du tegumen.

Alloaepytus coscinophora (Pfitzner).

Dalaca coscinophora Pfitzner, 1914, *Ent. Rdsch.* **31** : 105 (de Nivac, Matto Grosso).
Dalaca coscinophora Pfitzner et Gaede, 1937, *in* Seitz, *Gross-Schmett. Erde* **6** : 1294, Pl. 100*b*.

Aepytus (*Alloaepytus*) *coscinophora* Pfitzner et Gaede ; Viette, 1950, *Bull. sci. Bourgogne* **13** (1950–1951) : 4, fig. 2.

Une série ♂ de quelques exemplaires du Matto Grosso xii.1929 (*R. Spitz*) et un ♂ Brazil : Matto Grosso, Nivac (exemplaire topotype).

Les relations entre *Al. coscinophora* (Pfitzner, 1914) et *Al. tesselloides* (Schaus, 1901) ne sont pas correctement établies. J'ai eu pour étude l'abdomen du type de Schaus, à l'U.S. National Museum, qui est malheureusement une femelle décrite du Paraguay et j'ai vu le mâle de Pfitzner au Senckenberg Museum, mais la différence de sexe des deux types interdit une mise au point correcte.

" As our knowledge increases, the definitions of species, genera, etc., become widened or restricted. The **definitions** change in scope, while the **name** which was valid for the original definition remains the same. This contrast between a stable nomenclature and a labile knowledge is a nomenclatorial evil and a source of much disagreement among systematists. If we tried to make the names as labile as is our knowledge of nature, the remedy would be worse than the evil. Albeit we cannot do away with the evil altogether, we are at least able to mitigate its severity by the application of a dose of common-sense."

(Jordan, K., 1903, *Novit. zool.* **9** (suppl.) : xix.)

" It may sound almost ridiculous, but it is nevertheless true, that in many cases the time one has to spend over the nomenclature of a form, in order to clear up nomenclatorial muddle and to find out what form authors have meant to designate with a certain name, equals or surpasses the time one can, for certain reasons, devote to the study of the natural history of the animal. Surely this is wrong. The Natural History of the animal being the subject of our science, the accessory subject of nomenclature should never have assumed such magnitude. It is waste of energy. However, we have patiently to bear the fruits of the sins of our forefathers in science, and those who come after us will again mutter bad language. One may kick, but one has to suffer."

(Jordan, K., 1903, *Novit. zool.* **9** (suppl.) : xv.)

A REVIEW OF THE CLASSIFICATION OF THE SUBFAMILY ARGYNNINAE (LEPIDOPTERA: NYMPHALIDAE). PART 2. DEFINITION OF THE ASIATIC GENERA.

By B. C. S. Warren.

With 4 Plates.

Introduction.

The first part of this work, defining the European genera (Warren 1944), was shortly followed by the work of dos Passos and Grey on the Nearctic species (1945). Since then the desirability of extending my work to cover the Palearctic species has been obvious. In a further paper (Warren, dos Passos and Grey, 1946) we defined the Tribe Boloriidi, our previous papers having disclosed the existence of two fundamentally different groups of genera (tribes) in the subfamily. This further emphasised the necessity of adjusting the accepted classification of the Asiatic species and led me to assent to the repeated requests of entomologists in Europe and Asia to deal with the Palearctic genera as a whole, even though I am not able at present to deal with the speciation of the great group of holarctic species of the genus *Clossiana* (s. str.).

In view of the necessity for continual reference to the plates in my 1944 work, I have for the greater part used the same terms for the various parts of the genitalia in the present paper, but in two cases I have adopted the terms used by dos Passos and Grey (1945). These are (1) " vanni " for the gnathal plates ([Warren 1944, Pl. 6, fig. 18, shown in natural position, as seen from above] and figs. 10 or 32 which show the vanni on edge, at right angles to their natural position) and (2) " crista " for the ventral, spinose branch of the proximal end of the harpe, as distinct from the dorsal branch which is always unspined. The crista is a characteristic feature, sometimes continuous with the head of the harpe, as in fig. 35, more often separated from the latter by the featureless costa, as in fig. 33. In two important cases, however, I have had to differ from them. The processes that spring from the vestigial, basal plate of the phallobase, assuming many characteristic formations, which I called the " wings of the phallobase " or simply " wings " (see figs. 1, 5, 9, 35 and 38, etc.), while dos Passos and Grey use the term " anellus ". The true anellus rises more or less at right angles to the phallobase on each side of the aedeagus, containing it, in many cases encircling it. The wings of the Argynninae lie horizontally in the same plane as the basal plate from which they originate and act as a support on which the aedeagus rests. They do not give it lateral support. As a specialisation of the basal plate they should be distinguished from the true anellus. The second case refers to what I have called the " head of the harpe ", i.e. the terminal, distal end. dos Passos and Grey use the term " dorsal arm " for this in general, but name it " digitus " in the genus *Speyeria*. It is such a striking feature of that genus that one can easily understand why they adopted this course. But the digitus is, in fact, the head of the harpe, with which a certain featureless portion of the external sheet of the clasper has amalgamated, producing a semirectangular process with spines at its extremity and edging its distal end (fig. 30). Its homology with the head of the harpe is unquestionable and this process assumes many equally characteristic formations in other genera, which would be just as deserving of a special name. One cannot contemplate such a multiplication of names for one feature, however, and a further objection is that the digitus type of development is not, as its authors supposed, peculiar to *Speyeria*, but appears in the Palearctic genus *Mesoacidalia* (fig. 29). The only difference between the two formations is that the terminal point runs distad in *Speyeria* and ventrad in *Mesoacidalia* which, however, brings the terminal, spinal armament into the same position in both. This development of the harpe head in *Mesoacidalia* has been overlooked owing to its ventral line appearing in most illlustrations as a shadowy marking in the central area of the claspers, seemingly a portion of the internal sheet. When both internal and external aspects of the claspers are mounted so as to be seen together, the development of the harpe head becomes obvious, as in fig. 27. In some species of *Speyeria* the ventral edge of the harpe head is concave, not flat as in fig. 30, which causes the point to project more downward and, of course, results in a formation approaching that normal to the *Mesoacidalia* species. I may perhaps add that I continue to use the term " harpe " for the dorsal process of the claspers in its entirety, i.e. made up of the two proximal branches, the dorsal branch and the crista, the terminal process, i.e. the head, and the connecting median area known as the " costa ". These are all parts of one inseparable whole, none of which can operate independently. The reality of this is emphasised in a very remarkable manner in *Argyreus niphe*, the component parts being fused into a single, tubular structure (fig. 38) that can operate independently from the ventral portion of the claspers.

In this work the order of genera, now based on a complete view of the Palearctic species, shows some changes from the order I used in 1944. Contrary to what one had been led to expect, in only one instance in the tribe Argynnidi has a species become so isolated that it has lost all generic affinity with any other existing species. In this review I have tried to include the true subspecies, some of which have often been classified as species. Unfortunately, several species have suffered from uncontrolled race naming. A large number of these " races " are but variations of other races with which they fly. It cannot be too often repeated that true subspecies, or geographical races, exclude all other subspecies from the area of their distribution.

Subfamily ARGYNNINAE.

Dorsal area of ninth tergum membranous (non sclerotised) centrally ; terminal (distal) process of harpe external to the clasper.

Tribe BOLORIIDI.

Proximal end of aedeagus closed. (Warren, dos Pasos and Grey, 1946.)

(1) *Boloria* Moore.

Moore, 1900, *Lepid. Indica* 4 : 243 ; type *Papilio pales* [Denis and Schiffermüller].

As defined (Warren 1944 : 25). Includes four species : *B. pales* ([Denis and Schiff.]) ; *B. napaea* (Hoffmsg.) ; *B. graeca* (Stg.) and *B. sifanica* (Gr. Gr.). The latter has been proved to be a distinct species (du Cormier, Guérin and de

Toulgoet, 1953) and the following subspecies must therefore be removed from *B. pales* and placed with *B. sifanica* (Warren, 1954): subspp. *sifanica*, *palina* (Frhst.), *palinoides* Reuss, *banghaasi* (Seitz), *aquilonaris* (Stichel) and *alethea* (Hemming).

(2) *Proclossiana* Reuss.

Reuss, 1921, *Ent. Mitt.* 10 : 190 ; type *Papilio aphirape* Hübner (= *eunomia* Esper).

As defined (Warren 1944 : 25). Includes one species : *P. eunomia* (Esper).

(3) *Clossiana* Reuss.

Reuss, 1920, *Ent. Mitt.* 9 : 192, footnote ; type *Papilio selene* [Denis and Schiffermüller].

As defined (Warren, 1944 : 25).

This genus still awaits complete revision. It contains a large number of species, many of which are little known. To obtain a really adequate material of these would require years, and without it any attempt at speciation would be little more than guess work. In their work dos Passos and Grey (1945) assumed that the species could be divided into two groups on the characters of the aedeagus. It must be recalled that they included all species of *Boloria*, *Proclossiana* and *Clossiana* in one genus, *Boloria*. The true *Boloria* and *Proclossiana*, however, differ so markedly in the formation of the claspers from *Clossiana* that their connection with the latter is no more than tribal. In species of the restricted genus *Clossiana*, the two aedeagal types are obvious, so far as our present knowledge goes. The formation in the typical group (*C. selene*, etc.) is of small size, the latero-distal margins of the aedeagal membrane weakly developed and but slightly sclerotised. In the second group (*C. titania*, etc.) the organ is considerably larger, relative to the total size of the genitalia, and the latero-distal membrane considerably expanded and strongly sclerotised (see Warren, 1944, Pl. 10, figs. 31, 33 and 34). Although it is possible to separate the Palearctic species, so far as I know them, into these two groups, the degree of development of the latero-distal membranous folds and that of the sclerotisation present is proportionate to the actual size of the organ, which leaves the possibility of species existing that would be in a transitional position. It therefore seems best, until the majority of the species and their numerous races are better known, not to attempt any further subdivision of the true *Clossiana*. The following Palearctic species are included : *C. selene* ([Denis and Schiff.]) ; *erubescens* Stg.; *iphigenia* Graes. and subsp. *sachalinensis* Mats., *freija* Thnb., *polaris* Bsd., *frigga* Thnbg., *dia* L., *gong* Obth., *jerdoni* Lang, *amphilochus* Mén. and subsp. *elatus* Stg., *thore* Hbn., *improba* Btlr., *euphrosyne* L., *chariclea* Schn., *titania* Esp., *angarensis* Ersch., *oscarus* Ev. I was fortunate in obtaining two specimens of the rare *sachalinensis* Mats., which enabled me to establish that it is a race of *C. iphigenia* Graes. It is distinguished from the latter by the heavier type of all black markings on both sides. This race has been held to be a distinct species and also attached as a race to several other species. It is a characteristic example of the uncertainty that surrounds many of the individuals of this genus.

(4) *Argyronome* Hübner.

Hübner [1818], *Verz. bekannt. Schmett.* (2) : 32 ; type *Papilio laodice* Pallas.

The definition given (Warren, 1944 : 29), requires slight emendation, following on the recognition that *ruslana* Motsch. is congeneric with *A. laodice*, and that both belong to the tribe Boloriidi.

Uncus highly specialised, slender and tapering over whole length, bent upwards at the point of union (ventral) of the lateral edges, and rising sharply to or above plane of ninth tergum, terminating in hooked tip directed ventrad ; *gnathus* wanting, but angular sclerites attaching to the ventro distal edges of the tegumen present, which are rudiments of *vanni* ; *wings of phallobase* massive, widely separated at base, expanding greatly to distal extremity ; *aedeagus* massive with the proximal end closed, expanded centrally, endophallic tube bearing dense spine mass, replacing aedeagal wall over distal half of length ; *claspers* highly complex, dorso-distal termination free ; *harpe* atrophied (figs. 1, 2, 3 and [Warren 1944, Pl. 3]).

Includes *A. laodice* (Pall.), with subspp. *ariana* (Frhst.), *japonica* (Mén.) ; and *A. ruslana* (Motsch.) with subsp. *lysippe* (Jans.).

The removal of these two large species from the tribe Argynnidi to the Boloriidi is one more reminder of how little importance attaches to mere size in any question of relationship. It should be noted that the basally-closed aedeagus, as opposed to the open one, that characterises the two tribes is far from being the only character that indicates the true affinity of these two species. In all Argynnid genera the elaborate development of the harpe is a characteristic feature. In *A. laodice* and *A. ruslana* the harpe, as noted, is atrophied ; three short, featureless prongs springing from the costa are all that remains of it. The crista is never present in the Boloriidi, but always in the Argynnidi.

Tribe ARGYNNIDI.

Proximal end of aedeagus open. (Warren, dos Passos and Grey, 1946).

(5) *Issoria* Hübner.

Hübner [1818], *Verz. bekannt. Schmett.* (2) : 31 ; type *Papilio lathonia* L.

As defined (Warren, 1944 : 26).

Synonyms : In addition to those given (Warren, 1944 : 26), there should be added ; *Prokükenthaliella* Reuss, (1926 : 435), type *A. excelsior* Btlr.; *Yramea* Reuss, (1920 : 192, footnote), type *A. cytheris* Drury ; *Chilargynnis* Bryk (1944 : 8), type *A. cytheris* Drury ; (**syn. nov.**). *Issoria* includes *lathonia* L., *gemmata* Btlr. with subsp. *altissima* Elw., *eugenia* Evrs. with subspp. *rhea* Gr.–Gr., and *montana* B.–H., the African *hanningtoni*-group, and the South American *cytheris*-group. The striking feature displaying affinity between all these widely-scattered species is the gnathal developments (see *I. lathonia* [Warren, 1944, Pl. 4, figs. 10 and 12]). In this species the ventral and lateral parts are more developed than in any other, but the vanni are in a rudimentary state. In both *I. gemmata* and *I. eugenia* the structure is more primitive. The vanni are united ventrally into a solid plate. Such a structure must, doubtless, have preceded the two movable plates known in other species. Dorsally, the gnathus in *gemmata* and *eugenia* is united to the uncus, forming a complete ring to the tenth segment (fig. 34). In this figure the united vanni can be seen below the gnathus. In the African and American groups there is further specialisation in the development of the gnathal processes. These species are outside the limits of this work, but I mention them as the presence of these processes indicates that all are members of this remarkable genus.

(6) *Brenthis* Hübner.

Hübner [1818], *Verz. bekannt. Schmett.* (2) : 30 ; type *Papilio hecate* [Denis and Schiffermüller].

As defined (Warren, 1944 : 26). The only members of the genus are the three European species, all of which spread far into Asia, *B. ino* and *B. daphne* reaching Japan.

(7) *Fabriciana* Reuss.

Reuss, 1920, *Ent. Mitt.* **9** : 192 ; type *Papilio niobe* L.

As defined (Warren, 1944 : 26, 27, and figured Pl. 5, figs. 13, 14 ; Pl. 6, figs. 15, 18 ; Pl. 7, fig. 21, (European races)). The Asiatic races are figured in the present paper (figs. 9 to 18, and 32).

There are four distinct race-groups (species) in this genus, which cover a large number of races. These have been separated into at least eight supposed species in the past. After detailed study of the Asiatic races I cannot find any morphological justification for such division. The four distinctly characterised species are : *F. niobe* (L.), *F. adippe* ([Denis and Schiff.]), *F. nerippe* (Fldr.) and *F. kamala* (Moore). *F. niobe* is distinguished by the short and stout wings of the phallobase, the tips of which are suddenly bent over at the termination, and the head of the harpe, which is slightly flattened and without spines on the under surface ([Warren, 1944, figs. 13 and 21] and figs. 13 and 15). Further, the point of the uncus is relatively, short and slender and tapers markedly to its extremity ([Warren, 1944, figs. 15, 16] and figs. 14 and 16). In *F. adippe* the wings are long and slender, curving outwards over the last third of their length (figs. 9 and 11) and the head of the harpe is long and clyindrical and spined all over. The uncus is longer and heavier, tapering less and but slightly reduced in width at the termination. The vanni are also larger on the average than in *F. niobe* ([Warren, 1944, fig. 17 ; and] fig. 10). These characters distinguish all races of both species throughout their great geographical range from West Europe and North Africa to Japan. *F. kamala* is a specialised species, the only form in the genus in which the uncus is without any trace of a crest (fig. 32) ; the wings are very slender in proportion to their length, and the head of the harpe remarkably long, more than half the total length of the harpe, and much less densely spined. Finally, the *F. nerippe* races constitute the most isolated group in the genus. The harpe head instead of being an extension of the costa is set at right angles on the upturned end of the latter (fig. 17) ; the wings are somewhat similar to the *kamala*-formation but stouter, and the uncus has an extremely high crest carried far over the total length, and a very short but deep terminal point (fig. 18). These four species are unmistakable. The races that have at times been separated from them as distinct species are : *elisa* Godt. [Warren, 1944, Pl. 6, fig. 15 ; Pl. 7, fig. 21], *auresiana* Frhst. (figs. 13 and 14), *jainadeva* Moore (figs. 15 and 16) and *taigetana* Reuss. A comparison of our figures shows it is impossible to distinguish the first three races from each other or from the subsp. *niobe*. Specialised habitat and superficial features have been the only reasons for their separation, so far as I can ascertain. The race *jainadeva* alone develops a type of uncus that might serve to identify it—the short terminal point and hooked tip, and the crest with its serrated edge—but similar variation occurs in *F. adippe* in Europe, together with more normal formations. It is, perhaps, for this reason that *jainadeva* has sometimes been placed with *F. adippe*, but unless the early stages are distinct from those of *F. niobe* there can be no valid reason for separating it from the latter. The same applies to the subsp. *elisa*, for it and the subsp. *niobe* are morphologically identical. It is noteworthy that the *elisa* of Corsica differs in size and colour from that of Sardinia, though perhaps not with complete constancy; this shows the susceptibility to environment that is a characteristic of all the *niobe* races. The African *auresiana* Frhst. has also been a cause of trouble. Reuss (1922) concluded it to be a mainland form of *elisa*, at the same time noting that Rothschild held it was probably a species and Reverdin had stated it differed from *adippe*. Reuss was correct in so far as *elisa* and *auresiana* are structurally identical, and remembering the difference between the Corsican and Sardinian *elisa* it is quite possible that *auresiana* is a further development of the same strain. Reverdin was, of course, accurate, as always, for *auresiana* is so clearly connected to *niobe* that it could not possibly be a race of *adippe*. Reuss's material of *taigetana* was lost during the war, so that all one can say is that, judging from his works, it seems probable it is a race of *F. adippe*.

The composition of these four specific groups will be as follows:

(i) *F. niobe* (L). includes: subspp. *niobe* L. (= *eris* Meig.), *elisa* Godt. and f. *stechei* Vogt, *auresiana* Frhst., *kuhlmanni* Seitz, *orientalis* Alph., *jainadeva* Moore, *gigantea* Stg. It should be noted that subsp. *niobe* L. is the form without the silver markings on the underside, which, as it happens, is far the most abundant type in most areas. Transitional specimens with some silver spots are frequent, but the complete development of the silver is only a form, for it does not occur to the exclusion of the typical type anywhere, so far as I can ascertain. All races vary greatly in size, and it is no uncommon thing to find specimens in the Alps that are no larger than subsp. *elisa* flying with others that are much larger.

(ii) *F. adippe* ([Denis and Schiff.]) includes subspp. *adippe* [Denis and Schiff.], *bajuvarica* Spul. with f. *mainalia* Frhst., *adelassia* Frhst., *chlorodippe* H.-Sch., *taigetana* Reuss, *taurica* Stg., *tianschanica* Alph., and *vorax* Btlr.

(iii) *F. nerippe* (Fldr.) includes subspp. *nerippe* Fldr. (= *megalothymas* Frhst.) with f. *chlorotis* Frhst. and *nerippina* Frhst.

(iv) *F. kamala* (Moore) is apparently only known in the typical race.

(8) *Mesoacidalia* Reuss.

Reuss, 1926, *Dtsch. ent. Z.* **1926**: 69; type *Papilio aglaja* L. (=*charlotta* Haworth)

As defined ([Warren, 1944: 28, Pl. 6, figs. 19, 20; Pl. 7, figs. 22, 23 and] figs. 19 to 29). In this genus there are again a great number of races and forms that fall into a few specific groups. There has been a marked tendency to ignore structural character in setting up species, as in *Fabriciana*. *Mesoacidalia* is distinguished by the formation of the claspers and the head of the harpe. The only approach to these features is found in the genus *Speyeria*. The characteristic development of the harpe head has already been mentioned, and the compact form of the claspers in general is also similar. The harpe head varies in many races showing slight, inconstant peculiarities (see figs. 24, 25, 26, 27 and 29). Two characters are, however, constant to all races of *M. charlotta* : the harpe head rises slightly above the costa at the point of junction of the two, where the spines that cover the head begin, and the clasper develops on its distal surface a small, triangular protrusion, approximately mid-way between the apex and the ventral line. A similar little protrusion becomes highly accentuated in many species of *Speyeria*. These two distinctions are invariably present in the *charlotta* races. This is so in *alexandra* Mén., which in every respect is indistinguishable from the other *charlotta* races. The uncus (fig. 28) is typical, only varying in the extent of the serrations as do specimens of the typical subsp. *charlotta* in Europe [see Warren, 1944, Pl. 6, figs. 19, 20]. The genitalia in race *bessa* Frhst. (figs. 23 and 24) are slightly larger and the crest of the uncus more developed, but these features can be matched in European *charlotta*. The prominence of the terminal dorsal point of the claspers varies in most races ; it is, perhaps, most raised in the subsp. *lyauteyi* Obth. One would not be justified in separating race *bessa* as distinct on the strength of this degree of variability of the normal formation ; there is obviously even less reason for the separation of subsp. *alexandra*. *M. clara* (Blanch.) is a very distinct species, the type of uncus being unique (fig. 22), the harpe head, also, springing from the costa without any change of level and drooping down almost at right angles, bearing fewer but longer and more slender spines (fig. 20). *M. vitatha* is equally distinct, though less obviously so. The vanni are the most striking pecularity, being heavily corrugated, a formation I have not met elsewhere in the subfamily (figs. 19 and 21) (one vannus attached to the lower part of the tergum, the other to the harpe). The harpe head is also peculiar, bending down without upward curve and considerably shortened, not extending beyond the dorsal ridge of the clasper. The distal edge of the latter is without the protruding point. These characters are slight but constant and important, and distinguish *vitatha* very obviously, especially considering the unique type of vanni. The specific groups divide as follows :

(i) *M. charlotta* (Haworth) includes subspp. *charlotta* Haw. (= *emilocuples* Vty., W. and central Europe), *linnaei* Hemm. (= *aglaja* L., S. Scandinavia) with f. *boreas* Hemm. (= *emilia* Quenzel and *borealis* Stg., homonyms : N. Scandinavia), *mirabilis* Sag., *lyauteyi* Obth., *ottomana* Rob., *alexandra* Mén., *bessa* Frhst., *fortuna* Jans. with f. *myonía* Frhst.

(ii) *M. vitatha* (Moore), includes subsp. *vitatha* Moore with f. *ashreta* Evans. (I have not been able to dissect the latter ; it is placed here on the strength of its superficial features.)

(iii) *M. clara* (Blanch.) The only known race of this species.

(9) *Speyeria* Scudder.

Scudder, 1872, type *Nymphalis idalia* Drury.
Synonym : *Neoacidalia* Reuss, 1926, *Dtsch. ent. Z.* **1926** : 69 ; type *Papilio cybele* Cramer.

This genus is outside the scope of this work, the species being exclusively American. It is mentioned on account of its close affinity to the genus *Mesoacidalia*, so close that there can be no question that *Speyeria* has sprung from the latter. The remarkable type of harpe head, common to both (figs. 29 and 30) has already been referred to, also the similarity of the general formation of the claspers. In addition, two main types of uncus, one tapering the other of full width to the end, are present in both. I make no attempt to define *Speyeria*, but note the characters that distinguish *Mesoacidalia*. These are the marked dorsal curvature of the uncus in both types in *Mesoacidalia*, as contrasted with the almost flat ridge-line in *Speyeria*, and the harpe head, long and extending ventrad from the costa in *Mesoacidalia*, short and in continuous line with the costa in *Speyeria*.

(10) *Argynnis* Fabricius.

Fabricius, 1807, *Mag. Insektenk.* (Illiger) **6** : 283 ; type *Papilio paphia* L.

The definition of this genus (Warren, 1944 : 28) requires slight emendation owing to the inclusion of the Asiatic species *anadyomene*, which is congeneric with *A. paphia*.

Uncus long and slender, bent abruptly, close to base, upwards or downwards, tapering over all and terminating in a short, curved point ; *gnathus* represented by the vanni ; *wings of phallobase* simple, expanding continuously to blunt termination ; *aedeagus* broad at base, the aedeagal wall greatly reduced distally, replaced by dense spinal armament of endophalic tube, extending over two thirds of total length of aedeagus ; *claspers* terminating in dorso-distal, compound fold, bearing dense hair mass ; *harpe*, head free, short, thick and rounded, studded with short, coarse teeth ; *crista* of very similar proportions to the head, equally thickly studded with coarse teeth, ([Warren, 1944, Pl. 1, *A. paphia* and] figs. 4 and 5, *A. anadyomene*.)

It might be thought that the difference in orientation of the uncus in the two species indicated a difference in origin, but the uncal development is fundamentally the same in both. The presence of the teeth in *A. paphia* necessitates the downward bend, but in their absence the power of the uncal grip is much increased by the greater range and freedom of movement given by the elevation of the terminal claw in *A. anadyomene*. The teeth are extremely variable in length and number, and the shorter they are the more gradual is the depression of the uncus. Apart from the teeth, the development is on the same lines in both species ; the uncus is abnormally long, tapers regularly and gradually over all to the fine, strongly-curved, claw-like tip ; a combination of characters unique in the tribe. This can also be said of the highly specialised types of harpe head and crista. Both species are structurally very constant, and there can be little doubt that the genus is widely isolated from the others. *A. paphia* has developed surprisingly few subspecies, considering its great geographical range. It includes subspp. *paphia* L., *immaculata* Bell., *paphioides* Btlr., *megalegoria* Frhst. *A. anadyomene* Fldr. is only known in the typical race.

(11) *Childrena* Hemming.

Hemming, 1943, *Proc. R. ent. Soc. Lond.* (*B*) **12** : 30 ; type *Argynnis childreni* Gray.

Uncus broad, rectangular and of even width all over, terminating in a sharp tooth springing from dorsal ridge, which bears an extensive range of long hairs ; *gnathus* represented by strongly-developed vanni ; *wings of phallobase* simple but long, expanding centrally, terminating pointed ; *aedeagus* long and regular in width, endophallic tube dividing distally into two heavily-spined arms ; *claspers* complex, terminating in two rounded lobes covered with long hair-masses, the dorsal one developing a strong, short tooth, directed proxad ; *harpe* highly specialised in each species (figs. 31, 33, 35 and 37).

Includes *C. childreni* (Gray) with subspp. *childreni* Gray and *sakontala* Koll., *C. zenobia* (Leech), with subspp. *zenobia* Leech and *penelope* Stg. That two, otherwise closely connected, species show such specialisation in the development of the harpe is remarkable. The formation in *C. childreni* (fig. 33) reminds one of *Damora* (fig. 7) ; there is a style-like head, well-developed antistyle and an independent dorsal prong, but the long, powerful crista is more suggestive of *Mesoacidalia*. In *C. zenobia* (fig. 35) the harpe head and crista are united into a single process of considerable strength, covered with short, heavy teeth, The dorsal branch of the harpe remains normally developed, as does that in *C. childreni*.

(12) *Damora* Nordmann.

Nordmann, 1851, *Bull. Soc. Nat. Moscou.* **24** : 439 ; type *Damora paulina* Nordmann (= *Argynnis sagana* Doubleday).

Uncus elaborate, deep in proportion to length, terminating in a sharp, simple tooth springing from dorsal ridge, which also bears a number of short, broad teeth, directed distad over the entire length ; *vanni* weakly developed ; *wings of phallobase* simple in outline, uniform in width, with slight expansion at distal extremity ; *aedeagus* slender in proportion to length, endophallic tube bearing extensive armament of coarse spines that replace the aedeagal wall before the distal extremity ; *claspers* complex, termination rounded, with extensive, curved, dorso-distal fold, clothed with long hair ; *harpe* highly specialised, extensively united to clasper body, head replaced by style and developing short antistyle, studded with short teeth ([Warren, 1944, Pl. 2, *pandora* [Denis and Schiff.] and] figs. 6, 7, 8, *sagana* Dbld.).

Synonym ; Pandoriana Warren, 1942, *Entomologist* **75** : 246 ; type *Papilio maja*, Cramer (= *pandora* [Denis and Schiffermuller]). (**syn. nov.**).

In the two species of this genus we find another example of specialisation in the development of the uncus that obscures a fundamental identity of structure. The uncus in *D. sagana* has long been known as one of the most abnormal in formation, but the true nature of the structure has passed quite unrecognised. At the proximal end a heavy, crown-like object (that I shall refer to simply as the " crown " (see fig. 8)), rests on the dorsal ridge, and distad to this rise the teeth that are so familiar in *D. pandora*, but which range over the entire length of the uncus in the latter. In both species the uncus is deep, but the crest that springs from the dorsal ridge in *D. pandora* practically doubles the width. The crown in *D. sagana* produces a depth at the proximal end that equals the great depth of the crest in *D. pandora*. *Within the crown the proximal ridge-teeth are all fully developed.* Some of these can be seen in dark outline in fig. 8. The impossibility of teeth retaining their formation imbedded in a solid mass led to closer examination. This revealed that the crown is composed of two lateral pieces, rising from each side of the uncal crest and covering the teeth, which are fully developed along the ridge as in *D. pandora*. This unique structure is capable of opening as the uncus curves downwards, so exposing the teeth when required. When the uncus is released and returns to its normal position the crown closes again. As the teeth rise at right angles from the open crown it is not possible to mount them in that position, but I was able to mount the crown half open without depressing the teeth too much (see fig. 6). This mechanism is clearly an addition to the *pandora* type of uncus, and must have been evolved at a later date. In effect it supplies the uncus with retractile teeth. This crown is not the only peculiarity that exists in the genitalia of this species. The basal prong that exists internally on the claspers of many species is represented in *D. sagana* by two prongs (fig. 7), directed ventrad. In all other species this prong rises towards the harpe, that is in exactly the opposite direction. In fig. 7 the wings are seen also directed below the ventral edge of the clasper. This is merely owing to the pull of the membrane, which frequently causes them to turn over when mounting the claspers. The normal position is as usual in all species. The great spine mass of the endophallic tube in *D. sagana* is yet another characteristic of the species (fig. 7) but the characters of the harpe head, the spine system of the uncus and the wings all show close affinity with *D. pandora*.

D. sagana (Dbld.) includes subspp. *sagana* Dbld. and *liana* Frhst.

D. pandora ([Denis and Schiff.]) includes subspp. *pandora* [Denis and Schiff.], *pasargades* Frhst., *seitzi* Frhst.

(13) *Argyreus* Scopoli.

Scopoli, 1777, *Intr. Hist. Nat.*: 431 ; type *Papilio niphe* L.

Uncus short, slender and curving, tapering to distal, curved tip ; *gnathus* wanting ; *wings of phallobase* simple, very regular in width, extensively clothed with very fine scale-like points ; *aedeagus* regular in formation, endophallic tube heavily spined at distal end ; *claspers* complex, terminating partially duplicated, dorsal extremity extending beyond the basal, which is not completely sclerotised ; ventral edge recurved internally ; *harpe* highly specialised ; head, costa, basal branch and crista united in one semi-tubular process, covering dorsal ridge of clasper (figs. 38, 39).

A. niphe is the only representative of this genus. Structurally the only characters it has in common with the other genera are those of the tribe and subfamily. The extraordinary harpe which forms, as it were, a sheath over the dorsal edge of the clasper appears to be attached to the latter, but has in fact only a membranous connection. It is capable of independent, vertical movement.

CONCLUSION.

The genera defined in this paper, together with the Nearctic *Speyeria*, cover all known species of Argynninae. It has been shown that the subdivision of *Issoria* is unjustified, the various types of the primitive tenth abdominal segment testify to a close affinity which the world-wide distribution and complete segregation of many species has failed to obliterate. To any student of the subfamily the diversity and specialisation of morphological development will always be the most striking characteristic. In many cases the lines of evolution which have led to the highly specialised genera have also given rise to unique individual formations of most remarkable nature. Outstanding among these are the harpe in *Argyreus niphe*, capable of independent, vertical motion, the T-shaped harpe head in *Fabriciana nerippe*, the corrugated vanni in *Mesoacidalia vitatha*, and the uncal crown in *Damora sagana*, a mechanical contrivance for exposing teeth when required and recovering them after use. So far as I can ascertain none of these marvellous structures are known elsewhere in the Rhopalocera.

The " Fritillary " pattern is a subfamily characteristic. How it can for so long have been held to be a generic one is incredible. Such is the blinding power of colour and pattern, the two most impressionable and responsive elements to the forces of nature, and therefore the most unreliable as indications of relationship. One must assume that the " Fritillary " pattern has qualities of considerable protective value, and so has been maintained throughout two subfamilies ; the sudden break from it in the two most specialised genera, *Damora* and *Argyreus*, is of mimetic nature. This is a remarkable object lesson of how easily one meaningless appearance of similarity can be discarded in favour of another equally meaningless one. Both are efforts to disguise the true nature of the species. Colour, pattern and habits are indications of the conditions of life and nothing more ; morphology and embryology alone indicate relationship and the evolutionary lines of origin.

ACKNOWLEDGMENTS.

I have to express my sincere thanks to both Professor Teiso Esaki of Kyushu University and Professor Takashi Shirôzu of the same University, for much valuable material from Japan ; and to Professor Esaki for the trouble he took in obtaining rare species for me from the National Science Museum of Tokyo ; and to the authorities of that Museum for their valuable help. I have also to thank the authorities of the British Museum (Nat. Hist.) for the loan of a number of specimens with permission to dissect them.

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PLATE I.

Fig. 1.—*Argyronome ruslana.* Wings of phallobase and clasper. (Slide, B.C.S.W. 2014) Amur.

Fig. 2.—*Argyronome ruslana lysippe.* Tegumen and uncus. (Slide, B.C.S.W. 2011). Hokkaido.

Fig. 3.—*Argyronome ruslana.* Aedeagus. (Slide, B.C.S.W. 2014). Amur.

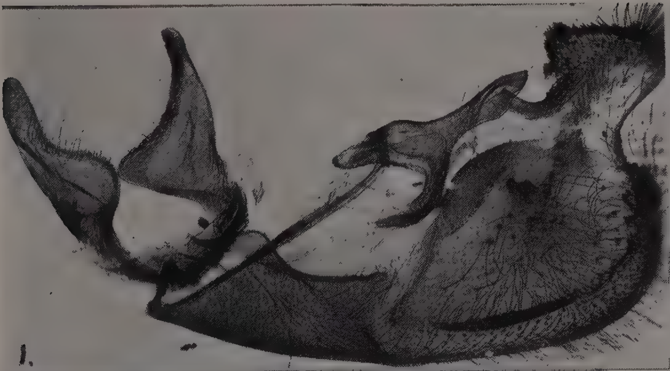
Fig. 4.—*Argynnis anadyomene.* Tegumen and uncus. (Slide, B.C.S.W. 1967). Mt. Inunaki, Fukuoka.

Fig. 5.—*Argynnis anadyomene.* Wings of phallobase and clasper. (Slide, B.C.S.W. 2023). Ishikawa, Honshu.

Fig. 6.—*Damora sagana liana.* Crown of uncus half open. (Slide, B.C.S.W. 1987), Oiwake, Shinano, Honshu.

Fig. 7.—*Damora sagana liana.* Aedeagus and clasper. (Slide, B.C.S.W. 1986). Kyushu.

Fig. 8.—*Damora sagana liana.* Uncus with crown closed. (Slide, B.C.S.W. 1986).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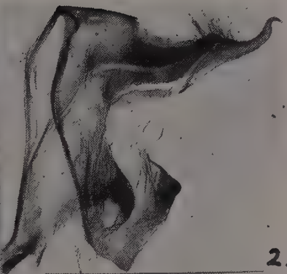
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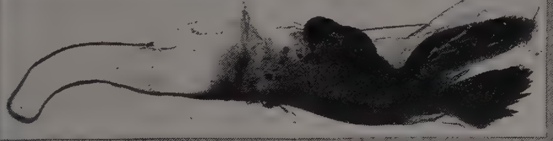
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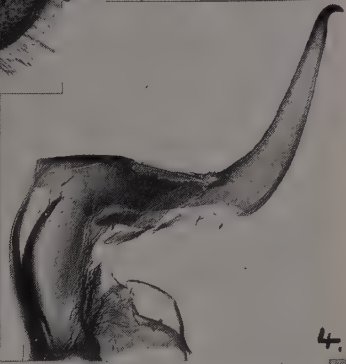
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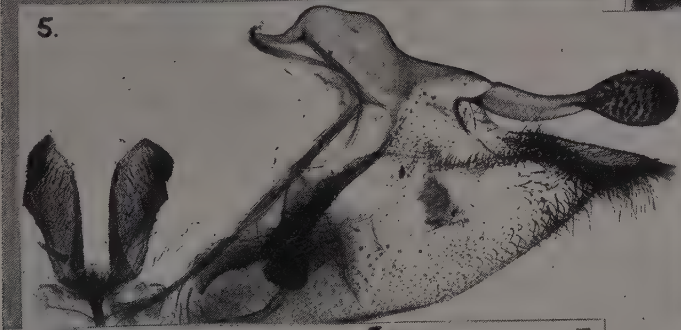
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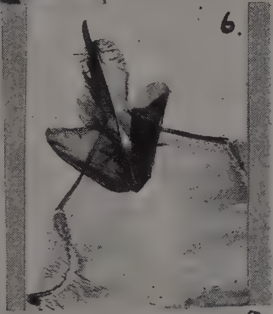
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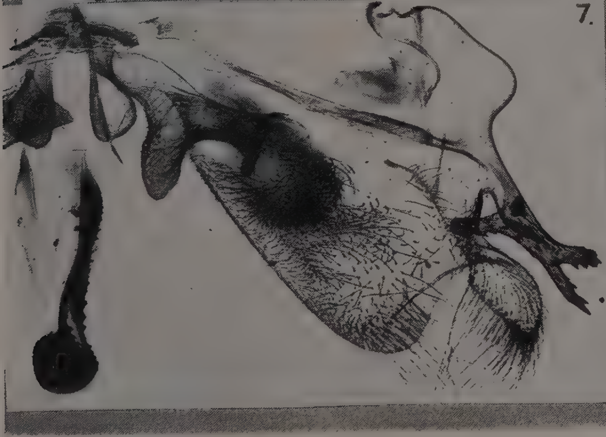
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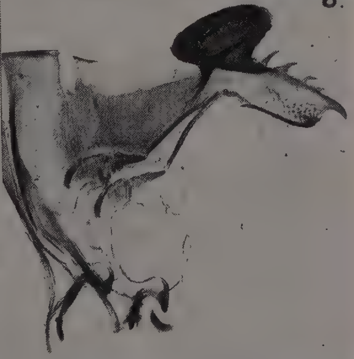
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PLATE II.

Fig. 9.—*Fabriciana adippe vorax*. Wings of phallobase and clasper. (Slide, B.C.S.W. 2016). Chang-Yang, 6000 feet.

Fig. 10.—*Fabriciana adippe vorax*. Uncus and vanni. (Slide, B.C.S.W. 2016).

Fig. 11.—*Fabriciana adippe tianchanica*. Wings of phallobase and clasper. (Slide, B.C.S.W. 2015). E. Turkestan.

Fig. 12.—*Fabriciana adippe tianchanica*. Tegumen and uncus. (Slide, B.C.S.W. 2015).

Fig. 13.—*Fabriciana niobe auresiana*. Wings of phallobase and clasper. (Slide, B.C.S.W. 2018). Lambèse (Powell).

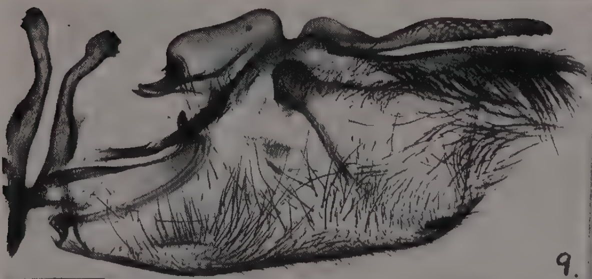
Fig. 14.—*Fabriciana niobe auresiana*. Uncus and vanni. (Slide, B.C.S.W. 2018).

Fig. 15.—*Fabriciana niobe jainadeva*. Wings of phallobase and clasper. (Slide, B.C.S.W. 2001). Rudugra Gael, C'tl. Himalaya.

Fig. 16.—*Fabriciana niobe jainadeva*. Uncus. (Slide, B.C.S.W. 2001).

Fig. 17.—*Fabriciana nerippe*. Wings of phallobase and clasper. (Slide, B.C.S.W. 1993). Kurosaki, Nr. Moji, Kyushu.

Fig. 18.—*Fabriciana nerippe*. Uncus and vanni. (Slide, B.C.S.W. 1993).



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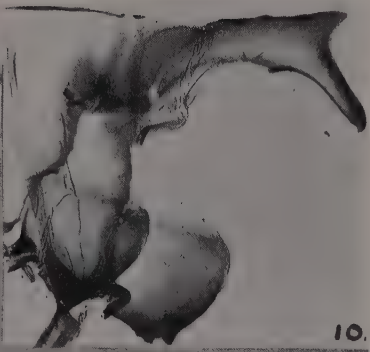

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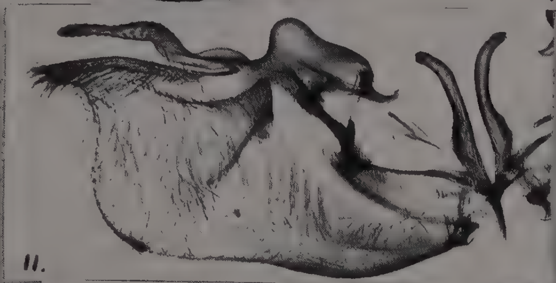

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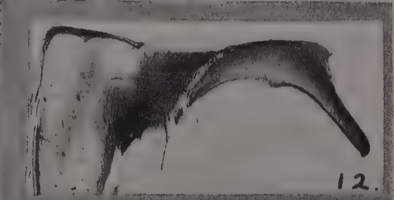

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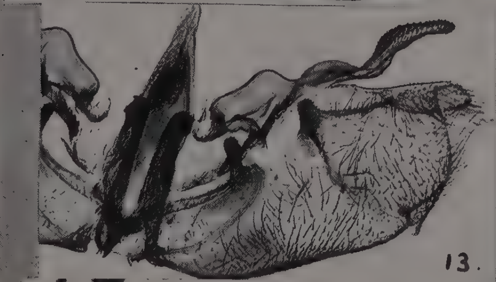

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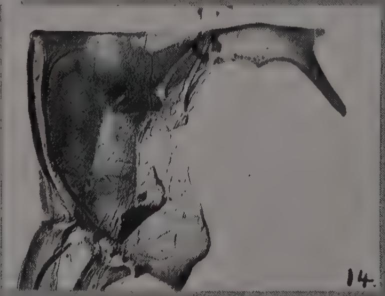

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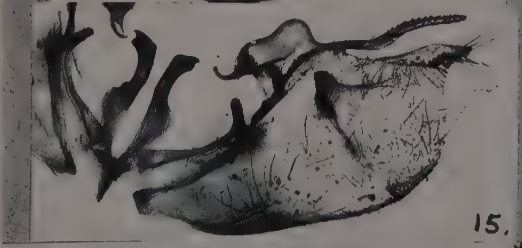

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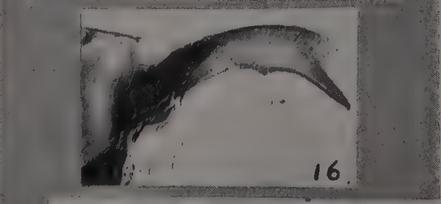

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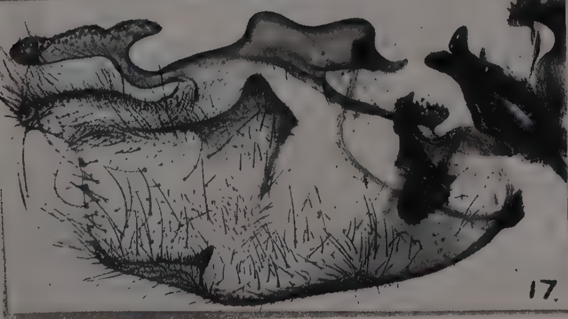

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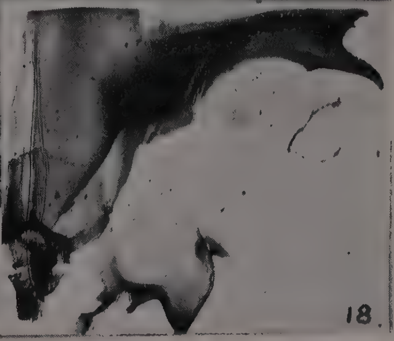

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PLATE III.

Fig. 19. *Mesoacidalia ritatha.* Clasper and vannus. (Slide, B.C.S.W. 2012). Mushkin, W. Gilgit.

Fig. 20.—*Mesoacidalia clara.* Wings of phallobase and clasper. (Slide, B.C.S.W. 2007). E. Tibet.

Fig. 21.—*Mesoacidalia ritatha.* Tegumen, uncus and vannus. (Slide, B.C.S.W. 2012).

Fig. 22.—***Mesoacidalia clara.*** **Uncus. (Slide, B.C.S.W. 2007).**

Fig. 23.—*Mesoacidalia charlotta bessa.* Tegumen and uncus. (Slide, B.C.S.W. 2009). Tse Kou.

Fig. 24.—***Mesoacidalia charlotta bessa.*** **Clasper. (Slide, B.C.S.W. 2009).**

Fig. 25.—*Mesoacidalia charlotta fortuna* f. *myonia.* Clasper. (Slide B.C.S.W. 2017).

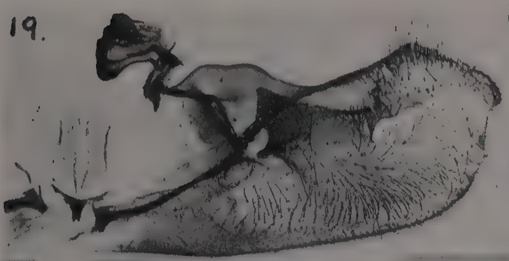
Fig. 26.—*Mesoacidalia charlotta alexandra.* Clasper. (Slide, B.C.S.W. 2008). Gulhek, Persia.

Fig. 27.—*Mesoacidalia charlotta fortuna.* Claspers: upper, internal view, lower, external. (Slide, B.C.S.W. 2028). Ut sukushigahara, Shinano, Honshu.

Fig. 28.—***Mesoacidalia charlotta alexandra.*** **Uncus. (Slide, B.C.S.W. 2008).**

Fig. 29.—*Mesoacidalia charlotta charlotta.* Harpe detached from clasper. (Slide B.C.S.W. 2022). Crowthorne, Berks.

Fig. 30. *Speyeria atlantis.* Harpe detached from clasper. (Slide, B.C.S.W. 1573). Enfield, Maine.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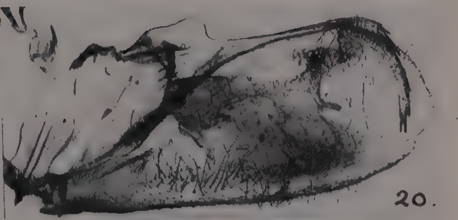
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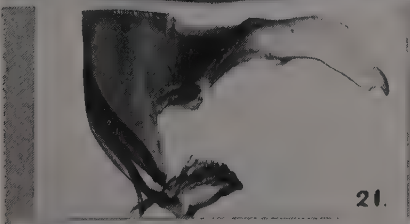
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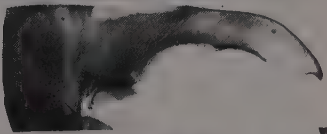
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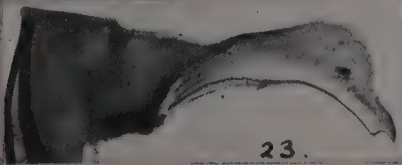
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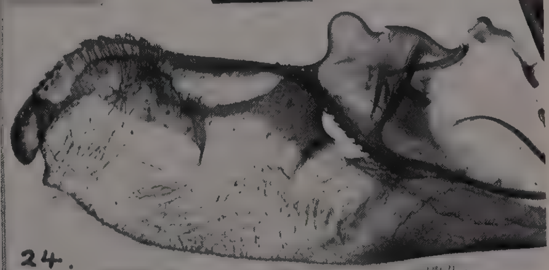
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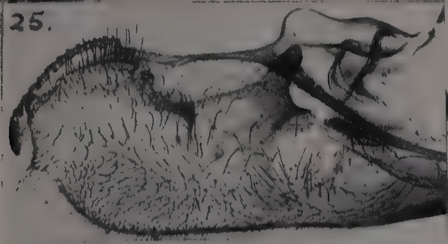
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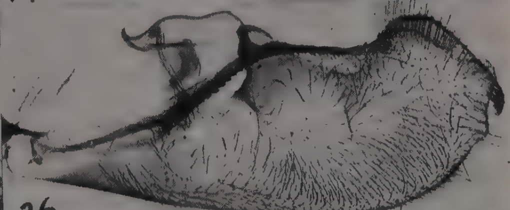
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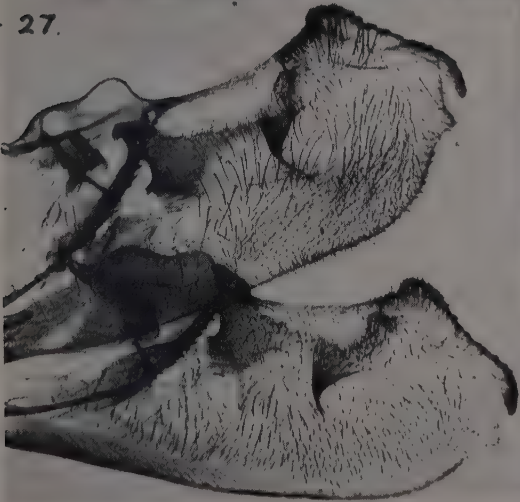
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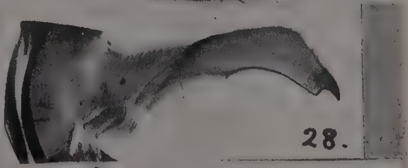
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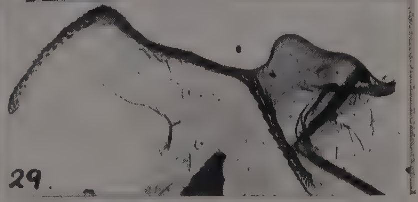
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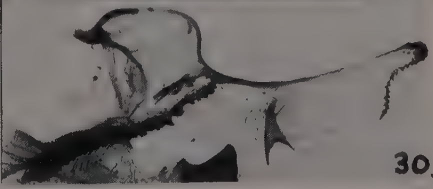
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PLATE IV.

Fig. 31.—*Childrena childreni.* Uncus and vanni. (Slide, B.C.S.W. 2002). Ta-tsien-lou.

Fig. 32.—*Fabriciana kamala.* Uncus and vanni. (Slide, B.C.S.W. 1569). Murree Hills.

Fig. 33.—*Childrena childreni.* Harpe and dorsal portion of clasper. (Slide, B.C.S.W. 2002).

Fig. 34.—*Issoria gemmata.* Uncus with gnathal process and clasper. (Slide, B.C.S.W. 2004). Teesta Valley, Sikkim.

Fig. 35.—*Childrena zenobia.* Clasper and wings of phallobase. (Slide, B.C.S.W. 2003). Ta-tsien-lou.

Fig. 36.—*Issoria eugenia.* Clasper and aedeagus. (Slide, B.C.S.W. 2005). Ta-tsien-lou.

Fig. 37.—*Childrena zenobia.* Tegumen and uncus. (Slide, B.C.S.W. 2003).

Fig. 38.—*Argyreus niphe.* Clasper and wing of phallobase. (Slide, B.C.S.W. 1994).

Fig. 39.—*Argyreus niphe.* Tegumen and uncus. (Slide, B.C.S.W. 1994). Kagoshima, Kyushu.

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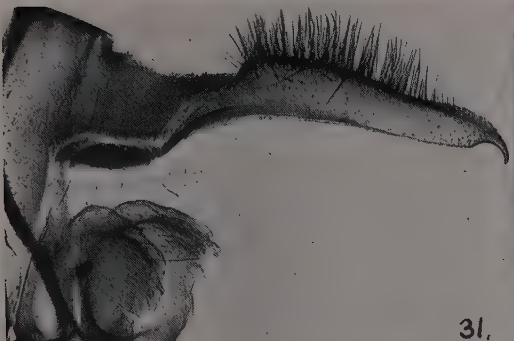

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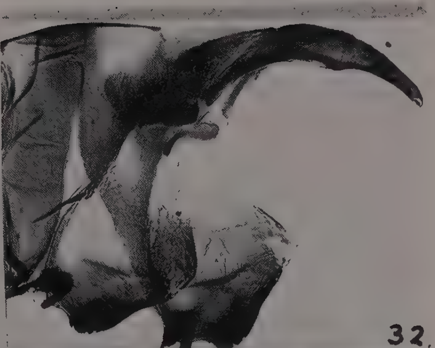

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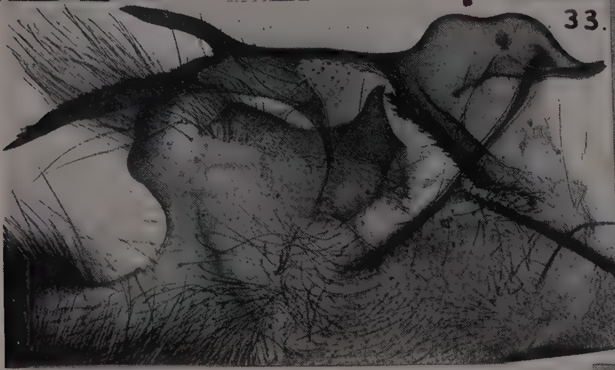

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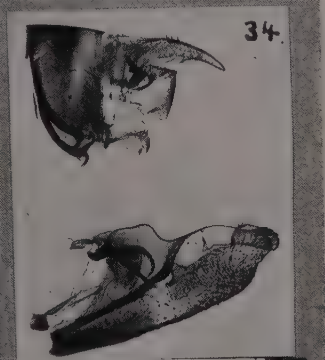

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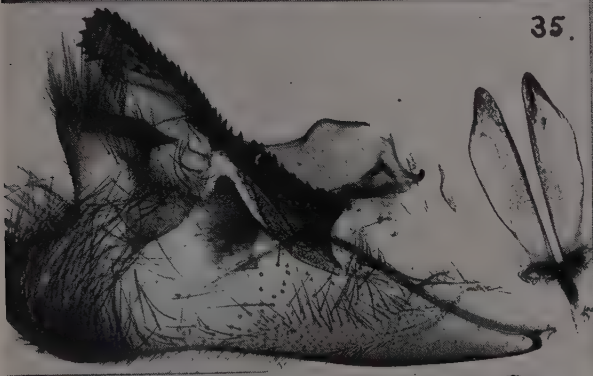

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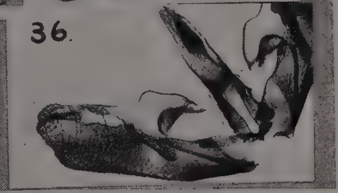

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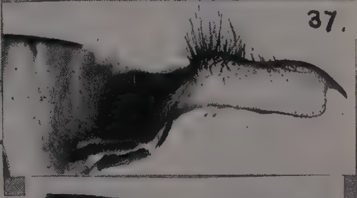

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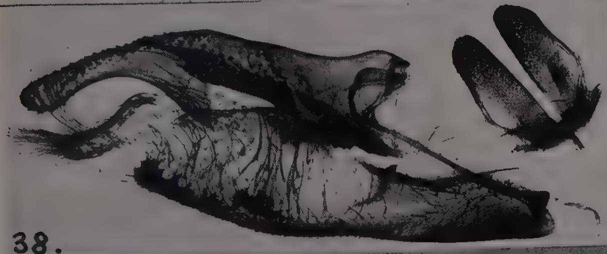

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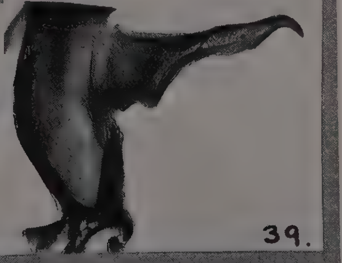

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